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Published at the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A., by the Society for Experimental and Descriptive Malacology.

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ON THE COVER -- Turridae from southeastern U.S.A. Illustrations by John L. Tottenham.

1989

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MALACOLOGICAL REVIEW

22 (1-2)

1989

VOLUMES, ISSUES AND PUBLICATION DATES OF MALACOLOGICAL REVIEW. - *Malacological Review* was first published in one number for the year 1968. This single issue (187 pages) constituted Volume 1. For each of the years from 1969 to 1974 (Vols. 2, 3, 4, 5, 6 and 7), two semiannual numbers were published, each two issues for a calendar year constituting a volume. Beginning with Vol. 4 (1971), each of the two annual issues were formally designated as a "number", the first issue of each volume being "Vol. _, No. 1" and the second issue "Vol. _, No.2". Beginning with Vol. 8 (1975), both issues for each calendar year were combined and designated as "Vol. _, No. 1-2". Each volume normally consists of about 200 pages.

Publication dates of past issues are as follows: Vol. 1, 7 June 1969; Vol. 2 [No. 1], pages 1-102, 10 June 1969; Vol. 2 [No.2], pages 103-214, 8 May 1970; Vol. 3 [No. 1], pages 1-102, 28 May 1970; Vol.3 [No. 2], pages 103-192, 13 March 1971; Vol. 4, No. 1, 27 July 1971; Vol. 4, No.2, 10 February 1972; Vol. 5, No. 1, 31 July 1972; Vol. 5, No. 2, 12 January 1973; Vol. 6, No. 1, 12 April 1973; Suppl. 1, 25 October 1973; Vol. 6, No. 2, 29 January 1974; Vol. 7, No. 1, 3 July 1974; Vol. 7, No. 2, 30 September 1974; Vol. 8, No. 1-2, 15 May 1975; Vol. 9, No 1-2, 26 March 1976; Vol. 10, No. 1-2, 3 March 1978; Vol. 11, No. 1-2, 20 July 1978; Vol.12, No 1-2, 21 December 1979; Suppl. 2, 31 October 1980; Vol. 13, No. 1-2, 30 April 1981; Vol.14, No 1-2, 22 July 1981; Vol. 15, No. 1-2, 4 May 1982; Suppl. 3, 15 July 1982; Vol.16, No. 1-2, 1 February 1983; Vol. 17, No. 1-2, 11 April 1984; Vol. 18, No. 1-2, 20 December 1985; Vol. 19, No. 1-2, 29 April 1987; Vol. 20, No. 1-2, 31 May 1988; Vol. 21, No. 1-2, 2 December 1988; Suppl. 4, 20 December 1988.

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Malacological Review, 1989, 22: 1-16

EARLY TERTIARY LAND MOLLUSKS (GASTROPODA: PULMONATA) FROM SIERRA SANTA EULALIA, CHIHUAHUA, MEXICO, AND THE ORIGINS OF THE NORTH AMERICAN ARID-LAND MOLLUSK FAUNA

Barry Roth and Peter K. M. Megaw

ABSTRACT

A thin lacustrine deposit in the Sierra Santa Eulalia, central Chihuahua, yielded a fossil land snail assemblage including the extant genera *Rabdotus* and *Holospira* and a helminthoglyptid (*Greggelix*?) similar to modern taxa of the arid American southwest. Three new species are described. Age of the fossils is probably 45-50 Ma. The assemblage indicates a mild to warm, moderately equable, and at least seasonally arid climate. As with plants, during the Tertiary, northern Mexico was a source of drought-adapted taxa ancestral to the present land snail fauna of the arid American southwest.

RESUMEN

En un delgado depósito lacustre de la Sierra Santa Eulalia, Chihuahua central, se colectaron gasterópodos fósiles de los géneros *Rabdotus* y *Holospira*, y un helmintoglíptido (*Greggelix*?). Todos ellos parecidos a formas actuales del árido sudoeste de los Estados Unidos. Se describen tres nuevas especies. Su edad probable es de 45 a 50 millones de años. La colección indica un clima de templado a cálido, moderadamente uniforme, y ocasionalmente árido. Así como en las plantas, durante el periódo Terciario, el norte de México fue la fuente de origen de moluscos adaptados a la aridez, ancestros de la fauna actual de los caracoles terrestres del árido sudoeste.

INTRODUCTION

Fossil land snails occur in a 2 m thick lacustrine deposit in a 1 km thick sequence of conglomerate, tuff, and welded tuffs approximately 20 km ESE of the city of Chihuahua, in the Sierra Santa Eulalia, Chihuahua, Mexico (Fig. 1). The fossiliferous bed is exposed in the north bank of the Arroyo Baltimore, about 200 m east of the Baltimore Shaft on the outskirts of the pueblo of Aquiles Serdan. Shells of the pulmonate gastropod *Rabdotus* weather out conspicuously; Hewitt (1968) cited them as "Paleocene and Eocene fresh-water terrestrial [*sic*] gastropods (identifications, courtesy of Instituto de Geologia, Mexico, D.F.)" but did not classify them more specifically or state the grounds for the age assignment.

The material reported here was collected by the junior author in January 1986 and September 1987. The assemblage is wholly different in taxonomic composition from coeval assemblages in Montana, Texas, and California. The latter contain elements of present-day mesic-temperate and tropical faunas, but the Santa Eulalia assemblage represents warm, less equable, and possibly semi-arid conditions. It suggests that during the Tertiary, northern Mexico was a source of drought-adapted taxa ancestral to the present land snail fauna of the arid American southwest.

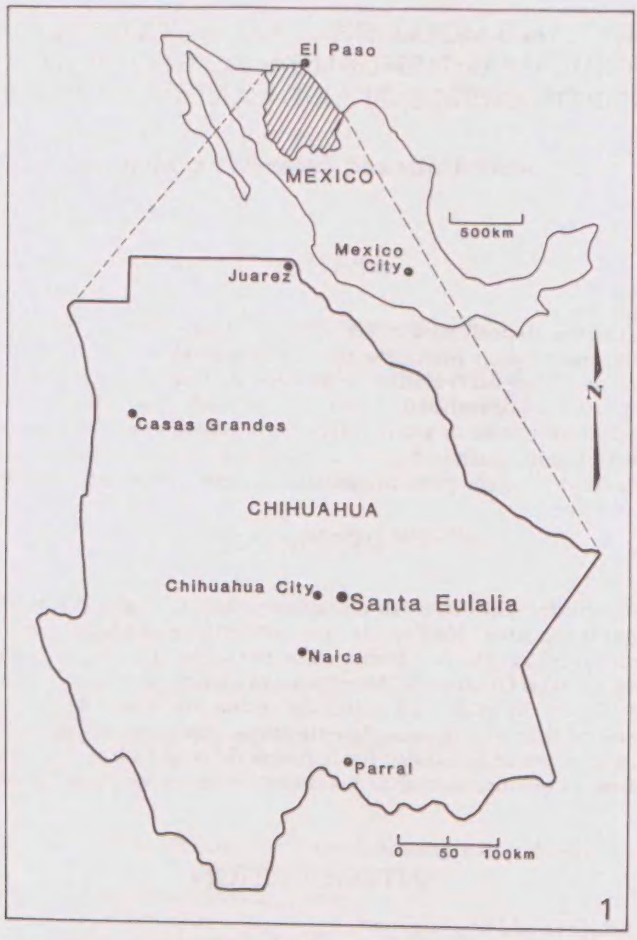

FIG. 1. Index map of Chihuahua, showing location of Santa Eulalia Mining District.

GEOLOGIC SETTING AND AGE

The Sierra Santa Eulalia contains the ore deposits of the Santa Eulalia Mining District, the largest carbonate replacement deposit in the world (Hewitt, 1968). Lower Cretaceous (Albian) limestones of the Finlay Formation are the oldest rocks exposed in the range (Lofquist, 1986). These were warped into a broad, doubly-plunging anticline during the Laramide Orogeny (Campa, 1985) and later deeply eroded. A 1 km thick package of conglomerates, tuff, and welded tuffs was then deposited, completely burying the rugged post-Laramide erosional surface. The fossils described herein come from a thin bed in the lower half of this package.

The conglomerates are composed of extremely poorly sorted, angular to subangular limestone and volcanic clasts that range in size from coarse sand to boulders 2 m in largest dimension. The matrix is tuffaceous; thin welded tuffs and andesite tuff beds are intercalated within the sequence. None of these volcaniclastic units has been radiometrically dated. The conglomerates show the rapid lateral and vertical facies changes typical of an alluvial fan environment.

The source of the sediments appears to have been from the north (Megaw, 1986), and the unit is probably correlative with the early Tertiary Pozos Formation described by Goodell (1981) in the Sierra Peña Blanca, 30 km to the north.

The Sierra Santa Eulalia was intruded by a quartz diorite body which apparently caused doming of both the Cretaceous limestone and the volcaniclastic package on the west side of the range (Megaw, 1986). This intrusion has yielded a K/Ar date of 37.8 ± 0.9 Ma (Megaw, in preparation). In the southern part of the range, the vocaniclastics are unconformably overlain by a 900 m thick section of welded tuffs erupted from the Santo Domingo Caldera (Megaw, 1986). The uppermost member of this ash-flow tuff package has yielded a K/Ar date of 31.7 ± 0.7 Ma (Megaw & McDowell, 1983).

These field relationships bracket the age of the fossils between the end of the Laramide Orogeny, 50-60 Ma before present (Clark & Ponce, 1983), and the time (ca. 38 Ma) when doming related to the quartz diorite intrusion occurred. The position of the fossils in the lower part of a 1 km thick unit deposited on a deeply incised erosional surface suggests that the fossil-bearing sediments were deposited somewhere in the middle of this interval, perhaps around 45-50 Ma before present (middle Eocene; Berggren *et al.*, 1985). Radiometric dating of the pre-caldera ash-flow tuffs intercalated with the conglomerates would allow finer resolution of the age of the gastropods.

The fossils were found in a bed composed of finely laminated, greenish andesitic tuff. The bed is bracketed by coarser sediments. Snail fossils (consisting of internal molds with substantial amounts of recrystallized shell material) are sparsely but uniformly distributed throughout the bed. The laminations probably indicate an ephemeral lacustrine environment into which the gastropods were washed during the waning stages of flood events. The gastropod assemblage consists entirely of terrestrial mollusks; no freshwater forms have been found. This also suggests that water accumulation may have been seasonal, or extraordinary, rather than perennial.

Type and figured specimens are deposited in the Departamento de Paleontología, Instituto de Geología, Ciudad Universitaria, Mexico (IGM), with additional specimens deposited as indicated in text.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Order Pulmonata

Family BULIMULIDAE

Genus *Rabdotus* Albers 1850

***Rabdotus hewitti*, new species**

(Figs. 2-5)

Diagnosis. A medium-sized, conical *Rabdotus* with apical angle of 45-55°, whorls moderately flat-sided, suture little impressed; base broad; peristome weakly expanded, columellar margin rolled tightly over umbilical region.

FIGS. 2-5. *Rabdotus hewitti*, new species. FIGS. 2, 3 holotype, IGM 4316, apertural and abapertural views; height 29.6 mm. FIG. 4, paratype, IGM 4317, lateral view; height 29.5 mm. FIG. 5, paratype, IGM 4318, apertural view; height 27.3 mm. FIG. 6. *Rabdotus alternatus* (Say), Recent, Laredo, Webb Co., Texas; apertural view; height 30.1 mm. FIG. 7. *Rabdotus* sp., cf. *R. hewitti*, IGM 4324, from same locality as holotype of *R. hewitti*; apertural view; height 24.2 mm (anterior end incomplete). FIGS. 8, 12-14. *Greggelix? hochbergi*, new species, holotype, IGM 4328, top, basal, and lateral views and oblique view showing color band; diameter 16.7 mm. FIGS. 9-11, 15. *Holospira plumbea*, new species. FIG. 9, paratype, IGM 4327, apertural view; height 16.9 mm. FIGS. 10, 11, 15, holotype, IGM 4325, abapertural, apertural, and lateral views; height 18.8 mm.

Description. Shell of medium size for the genus; spire straightly conical or very weakly convex in profile; apical angle 45-55°; whorls 5.75, moderately flat-sided, unshouldered, suture not deeply impressed; embryonic whorl sculpture not preserved; neanic whorl sculpture of weak collabral rugae, strongest below suture but often obsolete over most of shell, and occasional, stronger collabral rugae marking positions of former growth rests; base broad, short, narrowly perforate; aperture ovate; columella straight, without any folds or laminae; parietal wall with thin deposit of callus; peristome somewhat thickened and weakly expanded, columellar margin rolled tightly over umbilical region.

Dimensions of holotype. Height 29.6 mm, diameter 17.8 mm, height of aperture 15.2 mm, whorls 5.75.

Type material. Holotype, IGM 4316, CHIHUAHUA: north bank of Arroyo Baltimore, about 200 m E of Baltimore Shaft, Aquiles Serdan (approximately 20 km ESE of city of Chihuahua). Paratypes (7), IGM 4317-4323, from same locality as holotype. Additional paratypes deposited in University of California (Berkeley) Museum of Paleontology, U.S. National Museum of Natural History, Academy of Natural Sciences of Philadelphia, Field Museum of Natural History, and senior author's collection.

Remarks. *Rabdotus hewitti* resembles the Holocene *Rabdotus alternatus* (Say, 1830) from Texas and northern Mexico (Fig. 6) but is more broadly conic. The base is shorter and the columellar lip more tightly reflected over the umbilicus than in *R. alternatus*. *Rabdotus dealbatus neomexicanus* (Pilsbry, 1946) is similar but has more convex whorls and a more deeply impressed suture.

A few specimens have a shorter spire and proportionally larger body whorl (Fig. 7). These somewhat resemble the Holocene Baja Californian *Rabdotus pilula* (Binney, 1861) and may be a different species, but the present material does not provide enough evidence to separate them at this time. Considerable variation in spire height, even within local populations, is known to occur in modern *Rabdotus* (cf. Pilsbry 1946, figs., 6a, 6f, 7a).

The character of the umbilicus differentiates *R. hewitti* from *Orthalicus*, *Liguus*, and other conic Bulimulidae of more tropical affinities. In the subfamily Orthalicinae, the axis of the shell is imperforate at all stages of growth (Pilsbry, 1946). *Rabdotus hewitti* shows the characters cited by La Rocque (1960) that distinguish Bulimulidae from freshwater snails of the family Viviparidae: thin shell, last whorl longer than the spire, thin callus deposit on parietal wall, and peritreme interrupted by the parietal wall. There are no traces of the weak spiral ribs or keels present in many viviparids.

The earliest previous record of snails of the genus *Rabdotus* is that of *Rabdotus dealbatus* (Say 1821) in deposits of Blancan (late Pliocene-early Pleistocene) age in Palm Beach County, Florida (Taylor, 1966). All other fossil occurrences are Pleistocene or Holocene and involve living species, generally within the present ranges of their respective taxa (Christensen, 1978).

Bulimulid land snails are moderately widespread in Paleogene deposits of the Rocky Mountains. Most have been assigned to the genus *Oreoconus* Taylor 1962 (McKenna *et al.*, 1962; Taylor, 1975; Hanley, 1976). The "*Bulimulus*? sp." of La Rocque (1960) from the middle or upper part of the Flagstaff Formation, late Paleocene of Utah (Hintze, 1973), appears to be another species of *Rabdotus*, similar to *R. hewitti* but with the body whorl occupying more of the total height.

Etymology. The species is named for William Paxton Hewitt in honor of his pioneering studies on the geology of the Santa Eulalia District.

Family UROCOPTIDAE

Genus *Holospira* Martens 1860

Holospira plumbea, new species

(Figs. 9 - 11, 15, 16)

Diagnosis. A medium-sized, thick, weakly convex *Holospira* with fine, oblique axial riblets; aperture ovate, thick-lipped, peristome appressed to penultimate whorl; plane of aperture at angle to axis.

Description. Shell of medium size for the genus, cylindric-ovate, of approximately 10 rather tall whorls, with a beehive-shaped apex, weakly convex profile, and fine, oblique axial riblets apparently paralleling lines of growth; body whorl constricted behind aperture, base narrow and elongate but not keeled, umbilicate; aperture broadly ovate, peristome appressed to penultimate whorl, oblique; plane of the aperture at an angle of 20-35° to axis of shell; peristome turned outward in thick flange, somewhat revolute along basal margin. Internal column slender, hollow in later whorls, smooth at first but later with a single axial lamella.

Dimensions of holotype. Height (exclusive of expanded lip) 18.8 mm, diameter 6.5 mm, whorls 10.0.

Type material. Holotype, IGM 4325, CHIHUAHUA: north bank of Arroyo Baltimore, about 200 m E of Baltimore Shaft, Aquiles Serdan (approximately 20 km ESE of city of Chihuahua). Paratypes (2), IGM 4326 and 4327, from same locality as holotype. Additional paratypes in University of California (Berkeley) Museum of Paleontology.

FIG. 16. *Holospira plumbea*, n. sp., paratype, IGM 4326; longitudinal section showing axial lamella (a); height 10 mm.

Remarks. No specimen at hand has the embryonic whorls perfectly preserved, but the apex does not seem to have been mamillate. The description of the internal column is based on a ground longitudinal section of paratype IGM 4326 (Fig. 16). *Holospira plumbea* differs from most modern species in having the

upper limb of the peristome appressed to the penultimate whorl rather than free-standing. The oblique plane of the aperture is also unusual; the terminal phase of growth in most modern *Holospira* brings the plane of the adult peristome approximately parallel to the face of the spire.

The most similar Holocene species are members of the subgenus *Haplocion* Pilsbry 1902. These have relatively large shells with comparatively few, high whorls and the internal column slender, plain throughout or with an axial lamella in the penult (Pilsbry, 1946, 1953). A parietal lamella occurs in one species, *H. picta* Bartsch 1925. *Holospira* (*Haplocion*) *pasonis* Dall 1895 (type-species of the subgenus), from western Texas and northern Chihuahua, differs from *H. plumbea* in having a simple internal column, a peristome that is adjacent to but not appressed to the penultimate whorl, and 11.5 to 12 whorls. Other species of the subgenus have more elaborate terminal growth phases, producing remote peristomes, constricted and redirected body whorls, and stronger body-whorl sculpture; most have from 12 to 14 whorls.

Holospira plumbea differs from the *Holospira*? of McKenna *et al.* (1962, fig. 5) from the Bridger Formation, upper middle Eocene (late Bridgerian "Age") of Wyoming, in being larger, with fewer whorls and a weakly convex, rather than parallel-sided, profile. *Holospira grangeri* Cockerell 1914, from the Nacimiento Formation, Paleocene (Torrejonian or Puercan "Age"; Hartman, 1981) of New Mexico, is only about 10 mm high at a growth stage of ten whorls. Cockerell's (1914) comparison of *H. grangeri* to the Holocene *Holospira ferrissi* Pilsbry 1905, suggests that *H. grangeri* belongs to the subgenus *Bostrichocentrum* Strebel 1880, which includes smaller, shorter-whorled species. *Holospira eva* Gardner 1945, from the Oligocene of Tamaulipas, Mexico (Gardner, 1945), has a palatal lamella and traces of parietal and columellar lamellae and has therefore been assigned to *Holospira, sensu stricto* (Pilsbry, 1953).

In Russell's (1955, fig. 4) hypothetical restoration, *Holospira adventicia* Russell 1955, from the Kishenehn Formation, Eocene of British Columbia, is similar in shape and size to *H. plumbea*; it is drawn as having two more whorls. Like *H. plumbea* it has a broad lip and oval aperture and the peristome is tangent to the penultimate whorl. However, *H. adventicia* has a prominent parietal lamella, and the photograph of the holotype (Russell, 1955, pl. I, fig. 7) shows an unusually tall body whorl, not typical of any modern *Holospira*.

Holospira dyeri Tozer 1956, from the St. Mary River Formation, upper Cretaceous of Alberta, differs from *H. plumbea* in having a more acutely tapering spire. It does not reach maximum diameter until the eighth whorl. In longitudinal section (Tozer, 1956, fig. 5), palatal and parietal lamellae are visible in addition to an axial lamella.

Pupa? *leidyi* Meek 1873, from the Eocene of Wyoming, has never been figured and type material is apparently lost (White, 1886; Tozer, 1956; J.W.M. Thompson, pers. comm., 1987). Meek's (1873) original description mentions "about fifteen" whorls and a shell wider above the middle than below--characters that suggest the genus *Coelostemma* Dall 1895 (type species *Holospira elizabethae* Pilsbry 1889), as much as *Holospira*. If the species belongs to *Coelostemma*, then topotypes (when collected) will show a broad, hollow internal column, smooth or with fine vertical riblets, and no axial lamellae.

The "*Holospira* cf. *H. leidyi*" from the lower part of the Flagstaff Formation, Paleocene of Utah (La Rocque, 1960), could be *H. plumbea* but better preserved material is needed for a determination. The species cited as "*Holospira* sp." (Dorr, 1969) from the Pass Peak Formation and as "*Holospira* n. sp. A" (Hanley, 1976) from the Wasatch Formation, both Eocene of Wyoming, is figured and described (with a species-name given) in an unpublished thesis (Hanley, 1974, pp. 191-196, pl. IX, figs. 13-16). It differs from *H. plumbea* in having a tapering spire and more than fifteen whorls. The aperture is relatively much smaller than that of *H. plumbea*, although similar in that the peristome is appressed to the penultimate whorl.

Family HELMINTHOGLYPTIDAE

Genus ?*Greggelix* Miller 1972

Greggelix? *hochbergi*, new species

(Figs. 8, 12-14)

Diagnosis. A medium sized, umbilicate, depressed-helicoid helminthoglyptid with 1 mm wide shoulder band; last 1/5 whorl descending, constricted behind lip; aperture broadly auricular, oblique; lip thickened and turned outward, encroaching slightly on umbilicus.

Description. Shell of medium size for the family, depressed-helicoid, solid, umbilicate, umbilicus contained about 5.5-6.0 times in diameter; spire low to very low-conic; apical angle approximately 150°; whorls 5.1-5.3; whorl profile low-convex and apparently somewhat tabulately shouldered; suture well impressed; embryonic whorl sculpture not preserved; neanic sculpture of rather coarse, oblique collabral rugae; base inflated, especially in juveniles, tumid around umbilicus; shoulder of body whorl with distinct, 1 mm wide spiral band, prolonging trajectory of suture; last 1/5 whorl descending, constricted behind lip, especially basally; aperture subcircular in juveniles to broadly auricular in adults (somewhat distorted by compression), strongly oblique, peristome at angle of 55° to vertical, lip thickened and turned outward, most strongly at base; inner lip encroaching slightly on umbilicus.

Dimensions of holotype. Diameter 16.7 mm, height 6.6 mm; whorls 5.3.

Type material. Holotype, IGM 4328, CHIHUAHUA: north bank of Arroyo Baltimore, about 200 m E of Baltimore Shaft, Aquiles Serdan (approximately 20 km ESE of city of Chihuahua). Paratypes (4), IGM 4329-4332, from same locality as holotype. Additional paratypes deposited in University of California (Berkeley) Museum of Paleontology.

Remarks. In its depressed-helicoid shape and narrow, spiral color band on the shoulder, this taxon resembles species of several Holocene helminthoglyptid genera of the arid southwestern United States and northern Mexico: *Sonorella* Pilsbry 1900, *Eremarionta* Pilsbry 1913, and the nominate subgenus of *Greggelix* Miller 1972. The deflected terminal stage of the body whorl and expanded peristome tangent to the face of the body whorl (adaptations that improve

aperture-substrate seal) are characteristic of snails of at least seasonally arid climates.

The generic assignment is provisional. Protoconch sculpture (diagnostic of some of the southwestern Helminthoglyptidae) and details of the original shape are not well preserved in the material at hand. Other southwestern helminthoglyptid genera (such as *Eremariontoides* Miller 1981) are distinguished on characters of the soft anatomy. The available shell characters of *G.? hochbergi* are consistent with *G.* (*Greggelix*). The paleoclimatic analysis that follows also considers results based on *Sonorella* and *Eremarionta*.

Various land snail fossils assigned with more or less confidence to Helminthoglyptidae are known from rocks as old as late Cretaceous (*Mesoglypterpes* Yen 1952; based on *M. sagensis* Yen 1952, from near Sage Junction, Wyoming). However, there are no records of any of the above-mentioned southwestern genera from earlier than the Pleistocene (Bequaert and Miller, 1973). The earliest similar fossil helminthoglyptid is *Helminthoglypta alfi* Taylor 1954, middle Miocene (Barstovian "Age") of southern California, which Taylor (1954) believed closely related to the modern *Helminthoglypta* species of the Mojave Desert. *Greggelix? hochbergi* differs from *H. alfi* in being larger, with 0.3-1.2 more whorls at maturity. The whorls of *H. alfi* are more convex and the last whorl is deflected downward for only the last twelfth of its turn.

Etymology. The species is named for F.G. Hochberg, Jr., in honor of his contributions to west American malacology.

Family uncertain

Pulmonate land snail, indet.

Description. A pyramidal or lenticular gastropod with low-conic spire, apical angle about 130°; whorls more tightly coiled than the preceding species; base umbilicate; aperture apparently unmodified. Diameter 12.0 mm, height 5.0 mm; 5.0 whorls.

Referred material. One specimen, IGM 4333, CHIHUAHUA: north bank of Arroyo Baltimore, about 200 m E of Baltimore Shaft, Aquiles Serdan (approximately 20 km ESE of city of Chihuahua).

Remarks. Internal whorl partitions are present, indicating a pulmonate rather than a prosobranch snail, but other diagnostic characters are lacking. The specimen has been apico-basally compressed so that the original profile of the body whorl is not determinable.

DISCUSSION

Paleoenvironment

The present climate of the Sierra Santa Eulalia is warm and arid, with normal annual precipitation of less than 40 cm. Mean annual temperatures are between 17.5° and 20°, and mean annual ranges of temperature are between 17.5° and 20° C. The normal mean temperature for January is 10° C; normal mean

temperatures for August are between 22.5° and 25° C (World Meteorological Organization, 1979).

At present, the genus *Rabdotus* has an extensive range in North America. Its northern limit reaches from Alabama, Tennessee and Kentucky westward through Missouri, Kansas, Oklahoma, Texas, New Mexico, and Arizona. The genus is present in most of the northern and central states of Mexico, although it is absent from northwestern Sonora and most of the state of Baja California. It apparently reaches its southern limits in Jalisco, Puebla, and Oaxaca (Christensen, 1978). The highest species diversity occurs in southern Baja California Sur, probably as the result of a local radiation (Christensen, 1978).

The two northwesternmost species of *Rabdotus* (from southern Arizona) and several species from Baja California Sur have recently been reassigned to the otherwise South American genus *Naesiotus* Albers 1850, based on protoconch sculpture and details of the genital anatomy (Hoffman, 1988). The exclusion of those species does not significantly alter the paleoclimatic implications of *Rabdotus*.

The present-day range of *Holospira* is similar to that of *Rabdotus*. Its northern limit extends from southeast Arizona to central Texas. Its southernmost occurrence is in Oaxaca (Bequaert & Miller, 1973). Well over 100 species have been described, many of very local distribution. Species diversity is highest on the Plateau of Mexico and adjacent parts of the United States (Pilsbry, 1946). *Holospira* are snails of sunny, dry exposures in limestone terrain, typically at elevations of 1200-2100 m. North of the Tropic of Cancer, in a more arid environment, they may live at lower elevations as, for instance, at 300-430 m near Hermosillo, near the northwest limit of the genus (Bequaert & Miller, 1973).

The modern range of *Sonorella* covers most of Arizona, the southwest corner of New Mexico, Trans-Pecos Texas, northeast Sonora, and the northwest corner of Chihuahua (Bequaert & Miller, 1973). *Eremarionta* extends from southeastern California and extreme western Arizona through northeastern Baja California and western Sonora to Isla San Esteban in the Gulf of California (Bequaert and Miller, 1973). *Greggelix* (*Greggelix*) occurs at scattered localities in Baja California, principally in the Sierra de la Giganta, where it is sympatric with *Rabdotus*.

Recent *Sonorella* and *Rabdotus* (or *Naesiotus*) occur together in the Santa Rita Mountains, Arizona (Miller & Reeder, 1984), and the ranges of the genera overlap in northeastern Sonora, northwestern Chihuahua, and southern New Mexico. *Holospira* and *Rabdotus* are sympatric over large areas of Mexico north of Oaxaca.

The thermal fields (Axelrod & Bailey, 1969) of *Rabdotus*, *Holospira*, *Sonorella* plus *Eremarionta*, and *G.* (*Greggelix*) are plotted in Fig. 17, based on the mean annual temperatures and average annual ranges of temperature within the modern geographic ranges of these genera (data from World Meteorological Organization, 1979). The fields of *Rabdotus* and *Holospira* overlap extensively. The zones where the thermal fields of all three taxa overlap suggest a range of paleoclimatic parameters for the Santa Eulalia assemblage: mean annual temperature between 14° and 24° C, average annual range of temperature between about 10° and 21° C. The warmer values and smaller annual temperature ranges

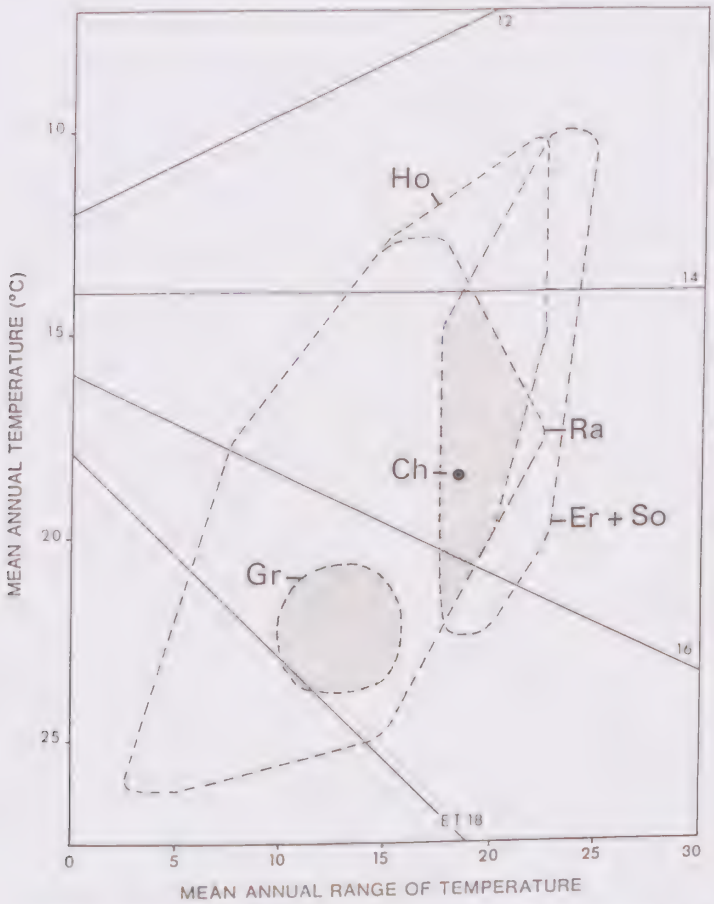

FIG. 17. Thermal fields of *Holospira* (Ho), *Rabdotus* (Ra), *Eremarionta* plus *Sonorella* (Er+So), and *Greggelix* (*Greggelix*) (Gr). Shaded areas define thermal relations inferred for Santa Eulalia fossil assemblage. ET, effective temperature in degrees Centigrade. Ch, present-day thermal parameters for city of Chihuahua, Mexico.

are derived from *G.* (*Greggelix*), the milder values and greater annual temperature ranges from *Sonorella* and *Eremarionta*.

Based on these data, nomographic analysis (Bailey, 1960; Axelrod & Bailey, 1969) produces an estimated effective temperature of 14° to 18° C (a mild to warm climate) with an equability rating of 48 to 55. At the warm extreme (based on *G.* (*Greggelix*)), there would have been 365 days per year warmer than 18° C and no freezing temperatures. Based on *Sonorella* and *Eremarionta*, the indications range from 244 days per year warmer than 16° C and temperatures below freezing during 5% of the hours of the year to, at the mild extreme, 183 days per year warmer than 14° C and temperatures below freezing approximately 0.5% of the hours of the year.

The modern distribution of *Sonorella* and *Eremarionta* includes the Sonoran Desert, where the snails inhabit rockslides in arid mountain ranges, but *Sonorella* also extends into the Transition and Canadian life-zones at higher elevations in Arizona (Pilsbry, 1939; Miller, 1967; Bequaert & Miller, 1973). Extremely xeric

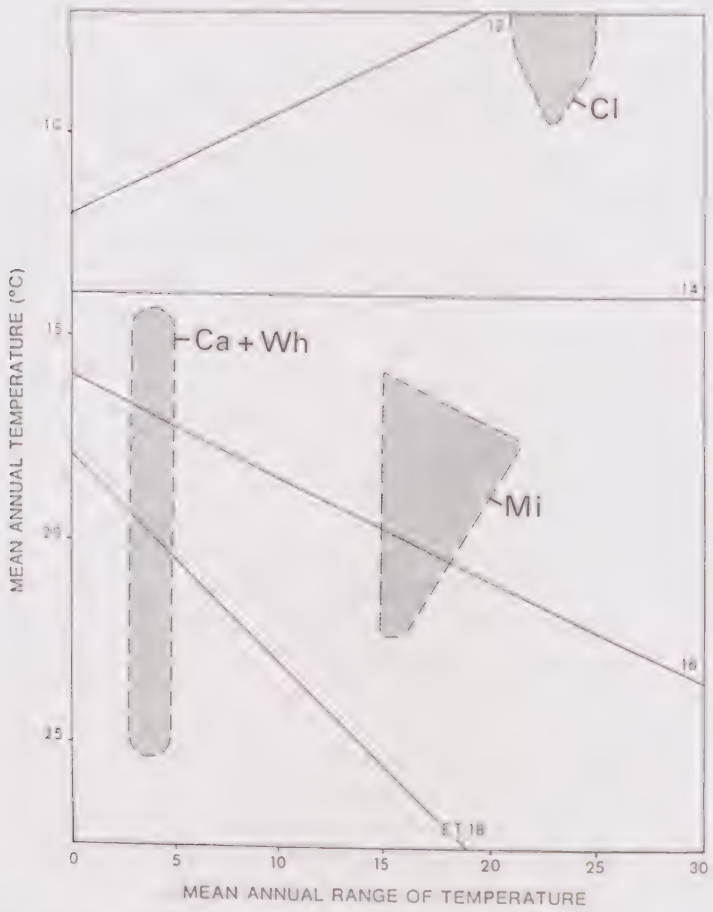

FIG. 18. Thermal fields inferred for Milligan Creek (Mi) and Climbing Arrow (Cl) Formations, Montana, and Candelaria and Whistler Squat local faunas (Ca+Wh), Texas.

conditions may not have been typical of the habitats of these genera through much of their existence. As an arid environment of regional extent, the Sonoran Desert is a relatively young feature, probably dating from late Tertiary and Quaternary time (Axelrod, 1979). Older environments of tropic savanna, dry tropic forest, short-tree forest, and drier plant formations contributed the ancestors of plant taxa that now characterize the desert. By analogy with vegetational history, the ancestors of *Sonorella* and *Eremarionta* probably inhabited relatively xeric sites in seasonally dry tropical or subtropical plant formations. *Greggelix* (*Greggelix*) now occurs in a zone of arid tropical scrub, outside the limits of the Sonoran Desert as defined by Axelrod (1979) and Wiggins (1980). Because of the suspicion that the modern climatic indications of *Sonorella* and *Eremarionta* are not quite typical in this respect, we favor a paleoclimatic interpretation based on *G.* (*Greggelix*) (Fig. 17).

Annual precipitation within the ranges of *Holospira* and *Rabdotus* varies from less than 30 to more than 120 cm/yr. Within the ranges of the three genera of Helminthoglyptidae, it ranges from 10 to 50 cm/yr. The field of overlap (ca. 30-50 cm/yr) might represent the annual precipitation for the Santa Eulalia

assemblage. However, as noted above, the present aridity of the Sonoran Desert is geologically recent and perhaps not typical of conditions over the ranges of these genera through much of the Tertiary.

Regional trends

Approximately coeval land snail faunas in North America include those from parts of the Vieja Group and Devil's Graveyard Formation, western Texas, and the Tejon, Scripps, and Friars formations in central and southern California.

The middle to upper part of the Flagstaff Formation in central Utah, thought to be of late Paleocene age (Hintze, 1973) contains probable *Rabdotus* and *Holospira* (La Rocque, 1960), although not at the same locality. These genera indicate comparable climatic conditions extending some 1500 km to the north 8 to 13 Ma prior to the deposition of the Santa Eulalia assemblage.

The Milligan Creek Formation of southwestern Montana (age ca. 42-43 Ma) contains the genera *Gastrocopta* and *Radiocentrum*, indicating a warm-temperate to paratropical climate with a minimum of 40 cm/yr precipitation (Roth, 1986). The Climbing Arrow Formation (age ca. 41 Ma), superjacent to the Milligan Creek Formation, contains the genus *Polygyrella*, which today inhabits mesic, forested parts of the Pacific Northwest. The indicated climate is cool-temperate, with about 50-75 cm/yr precipitation (Roth, 1986). The inferred thermal fields are shown in Fig. 18.

The Vieja Group and Devil's Graveyard Formation assemblages (Candelaria and Whistler Squat local faunas, ages 40 and 45 Ma, respectively) contain an element indicating highly equable, moist, and temperate conditions and other elements indicating tropical conditions. The genera are now extralimital, occurring either in temperate forest in Chiapas and Guatemala or in seasonal tropic forest in eastern Cuba or Central America (Roth, 1984). The inferred thermal field is shown in Fig. 18.

Camaenid land snails from the Tejon and Friars formations (age ca. 46 Ma) belong to genera now characteristic of the Caribbean region. They indicate a highly equable, tropical climate with precipitation between 80 and 200 cm/yr and seasonal drought (Roth, 1988). "*Helicina*" from the Scripps Formation (age ca. 46 Ma) is consistent with a mean annual temperature around 20° C and an average annual temperature range of less than 6° C; precipitation was probably about 140 cm/yr, with seasonal drought (Roth & Pearce, 1988).

Thus land mollusks indicate a period around 45 Ma of highly equable, moist (although seasonally dry), temperate to tropical conditions along the present Pacific coast and in present-day western Texas, while in northern Mexico, and perhaps as far north as southern Montana, mild to warm, less equable, and possibly semi-arid to arid conditions obtained. The 7.5- and 10-degree isotherms for annual range of temperature lay to the east between Santa Eulalia and western Texas and to the west between southern California and Santa Eulalia.

The greater annual temperature range at Santa Eulalia may have been the result of its more interior setting with respect to the coastlines of the time. Its greater aridity could have resulted from its being in the rain shadow of a proto-Sierra Madre Occidental. From the Cretaceous until 23 Ma before present, a volcanic arc existed at about the present site of the Sierra Madre Occidental

(McDowell & Clabaugh, 1979). Temporal variation, rather than paleogeographic setting, is another possible explanation for the differences among the assemblages. The rather loose temporal correlations now available (no direct radiometric or magnetostratigraphic age determinations have yet tied these disparate formations together) do not permit a choice between these alternatives.

Although Santa Eulalia is within the range of *Rabdotus* and *Holospira* today, the assemblage is equally consistent with the general southward retreat of land mollusk genera through the Tertiary observed in other North American faunas (Roth, 1984, 1986, 1988). The thermal parameters inferred for the assemblage are similar to those of more southern localities (e.g., Tamaulipas or Baja California Sur) in the modern ranges of *Rabdotus* and *Holospira* as well as to those around Chihuahua today. The northern limits of *Holospira* and *Rabdotus* were at least as far north as central Utah in the Paleocene, some 580 km north of their present range limits.

The character of the Santa Eulalia assemblage, as inferred from the modern climatic parameters of its component genera, is fully consistent with the model for plants (Axelrod, 1979, fig. 19) wherein northern Mexico served as a Tertiary center from which species adapted to seasonally dry, tropical conditions radiated to produce, ultimately, the arid-land taxa of today's American southwest. To the east and west, marine-influenced tropical climates hosted the ancestors of today's Central American-Caribbean tropical and mesic-temperate mollusk faunas.

ACKNOWLEDGMENTS

We are indebted to the management of Industrial Minera Mexicana, S.A., and Minerales Nacionales de México for the opportunity to work in the Santa Eulalia Mining District, especially Ings. Armando Ibarra A., Gilberto Marmolejo M., Juan Emilio Peña O., Dionisio Maldonado E., and Miguel Miranda G. Edna Naranjo García, James E. Hoffman, Walter B. Miller, María del Carmen Perrilliat, Jann W.M. Thompson and Joseph H. Hartman aided the study in various ways. We thank two anonymous reviewers for helpful criticism of the manuscript. Special thanks go to William Paxton Hewitt for his enthusiastic support of all aspects of Megaw's studies at Santa Eulalia.

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BARRY ROTH

Museum of Paleontology
University of California
Berkeley, California 94720 U.S.A.

PETER K. M. MEGAW

Department of Geology
University of Arizona
Tucson, Arizona 85721 U.S.A.

Malacological Review, 1989, 22: 17-23

MORPHOLOGICAL STUDIES OF A TAHITIAN SUCCINEID, *SUCCINEA (KONDOSUCCINEA) WALLISI*[1]

C. M. Patterson

ABSTRACT

A new succineid subgenus, *Kondosuccinea*, inhabiting Tahiti is described. *Kondosuccinea* is different from other *Succinea* in having a very long, convoluted penis (not a simple tube), which is emergent from the penial sheath for a large portion of its length. Both the penis and the vagina lack appendices. The penial retractor muscle is attached to the penial sheath and the epiphallus. Morphological and reproductive anatomical features are described for the type species, *Succinea* (*Kondosuccinea*) *wallisi* Cooke & Clench.

INTRODUCTION

The land snail fauna of Tahiti, particularly the genus *Partula*, is of interest due to the evolution of a large variety of endemic species within the confines of this relatively small volcanic island. Representatives of the pulmonate land snail family Succineidae are also found on Tahiti and it appears that they too have evolved to include some forms which are endemic to Tahiti. No work has been published on the Tahitian succineids beyond the description of several species based on shell characters only. Andrew Garrett (1884), in his excellent paper on the terrestrial mollusks of the Society Islands, stated that the determination of succineid species is "an almost hopeless task." However, he found four of the previously named Tahitian species (*Succinea humerosa, S. pudorina, S. costulosa, S. infundibuliformis*) and named a fifth species, *S. subglobosa*. Garrett also established the synonymy of the Society Island succineids and found that several had been incorrectly attributed to the Tahitian fauna.

The only other paper to focus on the Tahitian succineids is that of Cooke & Clench (1945), in which they described two new species and one subspecies (*Succinea wallisi, S. wallisi dolphin, S. amoi*). They also gave a more complete illustration of the shell of *S. bernardii* Récluz.

As previously discussed (Patterson, 1971), generic placement of succineid taxa is difficult when based solely on the shell, due to a great deal of convergent evolution worldwide. Anatomical features of the reproductive tract, and in some cases body form, appear to be the only valid morphological criteria for generic diagnoses. A description of some anatomical features of a remarkable endemic Tahitian succineid (*Succinea (Kondosuccinea) wallisi*) which represents a new subgenus is presented in this paper. The subgenus is named in honor of Dr. Yoshio Kondo who has devoted most of his scientific career to the study of Pacific land snails and has encouraged others to study them.

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[1] Field studies were supported by Grant No. 3974 and GB-6450 from the National Science Foundation to the Bernice P. Bishop Museum (Yoshio Kondo, Principal Investigator).

MATERIALS AND METHODS

Specimens were collected in 1970 by Dr. J. B. Burch. Specimens were relaxed in tap water and preserved in 70% ethanol with 1% glycerin. Anatomical dissections were done using a Wild M5 stereoscopic microscope and drawings made with the aid of a camera lucida. Jaws and radulae were dissected from the buccal mass and the remaining tissue removed by a brief treatment in NaOH. Radulae were observed using a compound microscope. Anatomical terminology follows H.B. Baker (in litt.).

RESULTS

Shell

Specimens used in this study were collected at the following localities on Tahiti-iti: (Lot 1970-159, collected on 8 July 1970) arboreal on plants along the Vaiteremu River in Ahoavini Valley and lot (1970-164, collected 10 July 1970) arboreal on plants along the Vaitio River in the Vaiarava Valley. Measurements of the largest specimen collected from each locality are shown in Table 1.

TABLE 1. Shell measurements of *Succinea (Kondosuccinea) wallisi* Cook & Clench.

Lot	Shell length	Aperture (=shell) width	Aperture length
1970-159	10 mm	6 mm	9 mm
1970-164	11 mm	7.4 mm	9.7 mm

The shell is ovate, glossy, thin, transparent, and light amber in color. There are 2 1/2 whorls with the body whorl greatly inflated (Fig. 1). The shell is flattened dorsoventrally. There is a slightly thicker, oblique, columellar plait with a flanged margin. Surface sculpture consists of only fine, unevenly spaced growth lines and faint spiral depressions, both producing an irregular surface. This description agrees with that of Cooke & Clench (1945). Voucher specimens from these lots have been deposited in the mollusk collection of the Museum of Zoology, The University of Michigan (cat. nos. UMMZ 250661 and 250662).

Jaw and Radula

The jaw (Fig. 2) is without ribs, amber in color with a deeply incised anterior margin on the cutting piece. The arms of the cutting piece are slightly pointed at the ends. The basal accessory plate has a slightly recurved margin. The radula has 10 lateral teeth on each side of the central tooth and from 22 to 50 marginal teeth. Such variation in the number of marginal teeth is common in many succineid species.

a

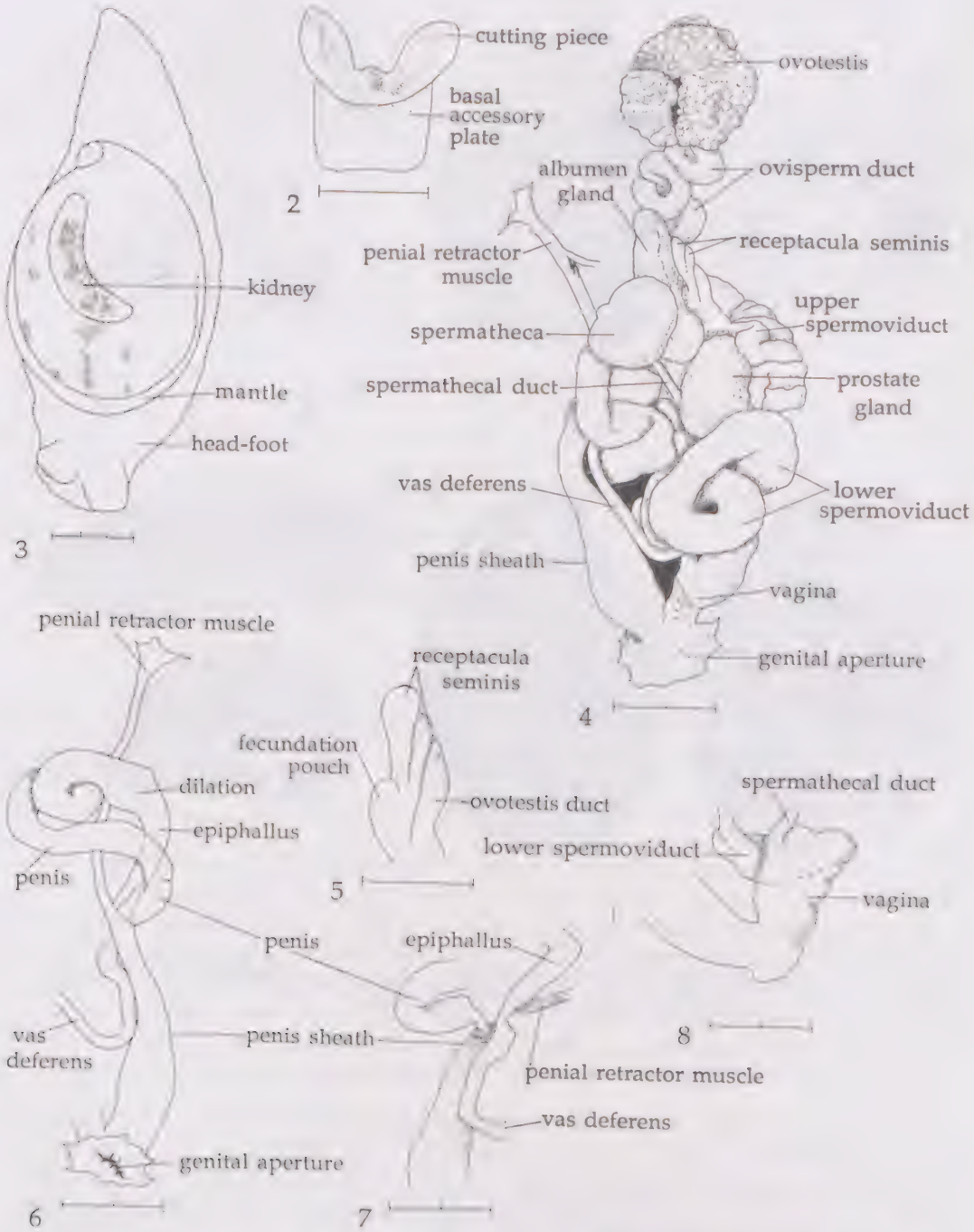
b

FIG. 1. Shells of *Succinea* (*Kondosuccinea*) *wallisi*. **a**, Holotype, BPBM 87027; **b**, UMMZ 250662. Measurement lines divided in millimeters.

Anatomy

The body of preserved specimens is translucent, white in color with prominent black pigmentation easily visible through the shell. The pigmentation pattern is variable but animals always appear to possess two stripes on the posterior, dorsal surface of the foot (Fig. 3) and on the head region. There are also patches of melanin over the white kidney and on the mantle border of the anterior and right side extending to slightly posterior of the pneumostome. The head-foot of the largest specimen dissected measured 22 mm in length and 5 mm in width.

A ventral view of the reproductive tract is shown in Fig. 4. The right tentacle assembly passes entirely proximal to the terminal genitalia (instead of between the penis and vagina as in most *Succinea* for which anatomical infomation is



FIGS. 2-8. Aspects of the anatomy of *Succinea* (*Kondosuccinea*) *wallisi*. Fig. 2. Jaw. FIG. 3. Headfoot and body. FIG. 4. Ventral view of the reproductive tract. FIG. 5. Receptacle seminis and fecundation pouch. FIG. 6. Terminal male genitalia. FIG. 7. Junction of the vas deferens and epiphallus cut free from penial sheath. FIG. 8. Terminal female genitalia. Measurement lines divided in millimeters.

available). The ovotestis is of moderate size, white in color with a scant amount of black pigmentation found mostly along the distal border with the overlying tissue of the digestive gland. The ovotestis occupies most of the terminal 1 1/2 whorls. The ovosperm duct emerges as a 1 millimeter long white duct which is closely appressed to the columellar side of the body wall. The duct then becomes larger, creamy in color, shiny, convoluted, and covered with a thin, slightly pigmented epithelium. The ovosperm duct terminates at the base of the albumen gland. There are two closely appressed receptacula seminis of unequal size (Fig. 5). A prominent fecundation pouch is also present (Fig. 5). The albumen gland is incompletely bilobed and creamy white in color. The acini forming the albumen gland are small and a single duct from the albumen gland joins a common channel which also receives the ducts from the ovotestis, fecundation pouch, vas efferens, and upper spermoviduct. The upper spermoviduct is flattened, compactly folded, and translucent white in color. There is a twist as the duct becomes the round, solid white lower spermoviduct. The lower spermoviduct is loosely folded with several convolutions. The inner wall of the spermoviduct has prominent longitudinal folds. The spermatheca is ovoid to spherical, thin walled, white in color with a long spermathecal duct which joins the spermoviduct near or at the junction of the most distal bend. In some specimens the lower spermoviduct is reflected anteriorly at the junction with the spermathecal duct (Fig. 8). The vagina is short and its distal portion has a shiny appearance due to the surrounding thick layer of strong circular fibers. The prostate gland is of moderate size, translucent white, follicular in appearance, and oblong-spheroid in shape. The vas efferens is short. The long vas deferens leads from the prostate gland, passes through an opening in the penial sheath and emerges as the tubular epiphallus (Fig. 7). There is a dilation of the epiphallus at the junction with the penis. The penis is here considered to extend distally from this epiphallial dilation. The penis is a long, slender, white tube with approximately 2/3 of its length emergent from the penial sheath. The emergent portion of the penis is convoluted and becomes progressively larger in diameter until it enters the upper portion of the penial sheath where it narrows abruptly (perhaps an artifact of fixation) due to constraints imposed by the small opening of the upper end of the penial sheath. The long, convoluted, emergent penis, is a very distinctive character of this *Succinea*, and an important characteristic on which the new South Pacific subgenus *Kondosuccinea*, described here, is distinguished. The anterior portion of the penis is enclosed in a sheath which is composed of 3 tissue layers which become very thick at the anterior end. The long penial retractor muscle has its origin on the penial sheath and epiphallus and inserts on the dorsal body wall just posterior to the anterior intestinal loop. The terminal common reproductive channel is extremely short and opens almost immediately to the outside as the genital aperture.

KONDOSUCCINEA, new subgenus

Diagnosis: *Kondosuccinea* is a group of South Pacific succineid species. These snails have a long, convoluted penis (not a simple tube), which is emergent from the penial sheath for a large portion of its length. Both the penis and the vagina

lack appendices. The penial retractor muscle is attached to the penial sheath and the epiphallus.

Type species: *Succinea wallisi* Cook & Clench 1945.

DISCUSSION

Island biogeography is of interest to evolutionary biologists because of the unique species which appear to have evolved in many island groups. Tahiti has its share of endemic species, including those belonging to the land snail family Succineidae. There are nine succineid species presently known to occur on Tahiti. These appear to belong to at least two morphologically distinct groups (subgenera). Most Tahitian succineids have not been found elsewhere and hence are believed to be restricted to Tahiti.

In all Pacific *Succinea* species studied with respect to reproductive antomy, the penis is entirely contained within the penial sheath. Another island form, *S. (Hyalimax) maillardi* (Fischer 1867) from La Réunion in the Indian Ocean, has only the upper end of the penis emergent from the penial sheath (Patterson, 1971), reminescent of some North American species. However, *S. maillardi* and *S. wallisi* are not related even though they happen to share a common characteristic (an emergent penis). *Succinea maillardi* has a slug-like body form with the mantle covering the shell, a unique jaw structure, and there are crystals on the inside wall of the short, blunt penis. None of these features are found among *S. wallisi* representatives. It is assumed that *S. wallisi* and its related species have evolved into a distinct South Pacific island group, probably endemic to Tahiti, for which it is useful to recognize a subgeneric classification.

It should be pointed out that *Succinea wallisi dolphin*, named as a new subspecies by Cooke & Clench (1945), is not associated with the subgenus *Kondosuccinea*, but rather with those species on Tahiti belonging to the subgenus *Succinea* s.s. Therefore, *S. wallisi dolphin* can no longer be considered a subspecies of *S. wallisi*.

Two individuals of *Succinea amoi* from the type lot were available for observation. Although the animals are contracted, it is readily apparent that they are related to *S. wallisi* since they exhibit the same long, convoluted, emergent penial structure.

ACKNOWLEDGEMENTS

I wish to thank Drs. J. B. Burch and Yoshio Kondo for the opportunity to study the field-collected specimens on which this paper is based. I also thank Dr. Kondo for loaning me the shell specimens from the collections of the Bernice P. Bishop Museum for comparison. J. B. Burch and Younghun Jung kindly photographed the shells. I am also grateful to S.-K. Wu for critically reading the manuscript.

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C.M. PATTERSON

Department of Biology
St. Mary's College
Orchard Lake, Michigan 48033
U.S.A.

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GROWTH AND FECUNDITY IN A BLACK-PIGMENTED AND AN ALBINO STRAIN OF *BIOMPHALARIA GLABRATA* (GASTROPODA: PULMONATA)

Marc Vianey-Liaud

ABSTRACT

Two strains of homozygous albino and pigmented Brazilian *Biomphalaria glabrata* were compared for 16 weeks. The rate of increase was significantly higher in the pigmented strain than in the albino strain. The differences between the mean shell diameter occurred during the first four weeks. The increase in the total body weight was linear. During the entire experiment, the pigmented snails were heavier than the albinos. The onset of egg laying was simultaneous in the two strains. When they reached sexual maturity, the diameter and the weight of the snails showed a large variability, but the pigmented snails were statistically larger and heavier than the albino strain. Fecundity (number of clutches, eggs, eggs per clutch, viable embryos and hatchability) was significantly higher in the albino strain than in the pigmented strain. Comparisons of growth or fecundity observed in the field or in the laboratory should take into account pigmentation of the snails if the observations concern snails of various genotypes.

INTRODUCTION

Numerous papers on *Biomphalaria glabrata* (Say) report growth curves or numerical data upon fecundity obtained in the field or in the laboratory (see reviews in Freitas *et al.*, 1975; Scherrer *et al.*, 1976; Vianey-Liaud, 1976; Chquiloff *et al.*, 1978; Pointier, 1982). The differences of growth or fecundity shown in various papers may be due to abiotic factors (Appleton, 1978), crowding or the mode of fertilization (selfing or crossing) (see review in Vianey-Liaud, 1976).

In natural populations, especially in Brazil, an albino phenotype coexists with various pigmented phenotypes (Newton, 1954, 1955; Paraense, 1955; Richards, 1967). These phenotypes are commonly present in laboratory stocks of Brazilian snails.

I have reared in the laboratory Brazilian *Biomphalaria glabrata* from 1969 to the present. From these stocks, using albinism as a genetic marker for experimental crosses, an albino and a black-pigmented strain have been isolated for three years. This paper reports comparative data on growth and fecundity of the two related strains, one albino and one black pigmented, reproducing exclusively by self-fertilization.

MATERIALS AND METHODS

The snail stocks bred in the laboratory are Brazilian *Biomphalaria glabrata* (from Northern Minas Gerais). From these stocks, albino and black-pigmented strains have been separated for three years. The two strains are homozygous: pigmented snails (PIG) - homozygous CC; albino snails (ALB) - homozygous cc (Richards, 1967).

Two lots of 30 immature snails of similar mean sizes and mean weights have been constituted. To prevent possible effects of crowding and of mode of fertilization, each of the snails of the two lots have been raised in isolation during the length of the experiment (16 weeks); thus, selfing is their only method of reproduction.

Growth was recorded weekly by measuring the shell diameter and the total wet weight. For determining the onset of egg laying, the clutches were recorded daily until all the snails had laid eggs. Later, when all the snails had reached sexual maturity, fecundity was observed twice a week. Fecundity has been defined by the numbers of clutches, of eggs, of eggs per clutch and of hatchability.

Snails were maintained at 25°C in artificial light (12 hrs light/12 hrs dark).

Analysis of variance and chi-square test were used to compare size, weight and fecundity between PIG and ALB. The ponderal growth of each strain was studied by an analysis of variance upon the regression (Lison, 1968).

RESULTS

Growth

At the beginning of the experiment (two weeks after hatching), the PIG and the ALB showed a similar mean shell diameter and mean total wet weight (Table 1).

Table 1. Shell diameter and total body wet weight of PIG and ALB *Biomphalaria glabrata* at the beginning of the experiment. The diameter is expressed in millimetres, and weight in milligrams.

Character	PIG n = 30	ALB n = 30	p
shell diameter	2.98 ± 0.04	2.94 ± 0.03	n.s.
wet weight	4.36 ± 0.25	4.26 ± 0.15	n.s.

n.s. = no significant difference.

Figs. 1 and 2 show that the absolute growth of ALB was lower than that of PIG. Size and weight were significantly ($p < 0.05$) superior in PIG as early as the first experimental week.

The difference between the increase of the mean shell diameter of PIG and ALB occurred during the first four weeks (approximately during immaturity) (Table 2). From the fourth to the sixteenth week, the diameters increased at the same rate in the two lots; the two curves were parallel and PIG remained significantly larger than ALB.

Growth, expressed by the total body weight, was linearly correlated with time in PIG and ALB. The linear terms of the regression are statistically highly significant, while the nonlinear terms are not significant. The weekly relative increase of weight was included between 31.4 and 35.0 mg in PIG and between 22.5 and 24.0 mg in ALB. The results are summarized in Table 3.

Onset of Egg Laying

The day when the first snail of the two lots laid the first clutch was considered as day zero. When each snail reached sexual maturity, three measurements were recorded: the delay from the first clutch (day zero), the shell diameter and the total body weight. The results are shown in Table 4.

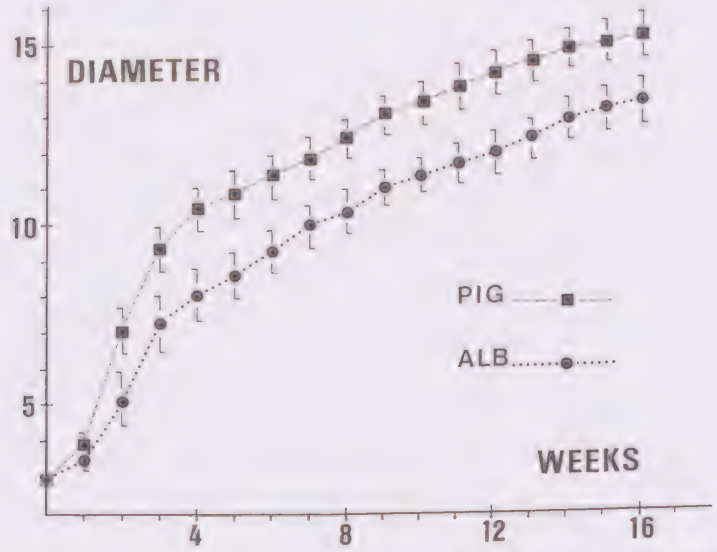

FIG. 1. Increase of the shell diameter in PIG and ALB *Biomphalaria glabrata* during 16 weeks. The diameter is expressed in millimetres. The fiducial limits of each mean are calculated for the level of probability p = 0.05.

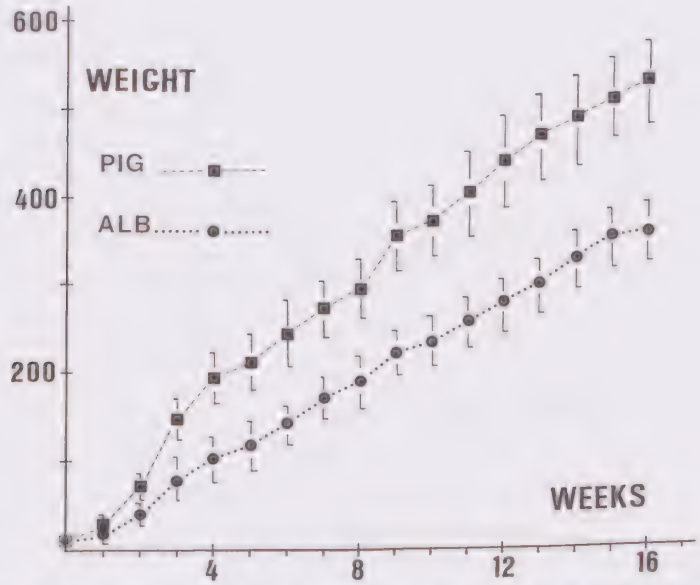

FIG. 2. Increase of the total body weight in PIG and ALB *Biomphalaria glabrata*. The weight is expressed in milligrams. The fiducial limits of each mean are calculated for the level of probability p = 0.05.

In comparison with ALB, the onset of egg laying in PIG was slightly delayed (about three days), but the difference is not statistically significant. As a consequence of differences in growth, as shown in the growth curves reported previously (Figs. 1, 2), the PIG are highly significantly larger and heavier than ALB when they deposit their first egg mass, although they are of a similar age.

Table 2. Comparison of the increase in shell diameter during 16 weeks, expressed in mm.

Snails	weeks 0 to 4	weeks 4 to 16
PIG n = 30	7.44 ± 0.32	4.74 ± 0.24
ALB n = 30	5.05 ± 0.37	5.34 ± 0.33
p	<0.001	n.s.

< 0.001 = significant difference to the level of probability p = 0.001; n.s. = no significant difference

Table 3. Analysis of the absolute growth, expressed by the increase in wet weight, in PIG and ALB, during 16 weeks.

	PIG	ALB	d.F.
r	0.55 < 0.05	0.84 < 0.01	15
LR	1270 < 0.001	1249 < 0.001	1 & 493
NLR	1.54 n.s.	0.43 n.s.	15 & 493
b	33.20	22.76	-
Sb	0.93	0.64	-
F.1.	31.4 < b < 35.0	22.5 < b < 24.0	-

r = correlation coefficient; LR = linear terms of the regression; NLR = non-linear terms of the regression; b = slope of the regression line; Sb = standard deviation of the slope; F.1 = fiducial limits of the slope calculated for the level of probability p = 0.05.; < 0.05 and <0.01 = correlation cofficient significant to the level of probability p = 0.05 and 0.01; <0.001 = linear terms significant to the level of probability p = 0.001; n.s. = non-linear terms not significant.

Table 4. Onset of egg-laying in PIG and ALB *Biomphalaria glabrata*.

Snails	Delay	Diameter	Weight
PIG n = 30	16.7 ± 2.1 (4 - 41)	10.9 ± 0.2 (8.3 - 13.4)	221.4 ± 12.6 (91 - 358)
ALB n = 30	13.0 ± 1.6 (0 - 34)	8.7 ± 0.2 (6.1 - 11.2)	119.4 ± 8.4 (42 - 227)
p	n.s.	< 0.001	< 0.001

The delay is expressed in days, the diameter in millimetres and the weight in milligrams. The values between brackets are the extreme data.
n.s. = no significant difference; <0.001 = difference statistically significant to the level of probability p = 0.001.

Table 5. Total numbers of clutches and eggs produced by PIG and ALB *Biomphalaria glabrata* during 16 weeks.

Snails	Clutches	Eggs	Abortive eggs	Viable eggs
PIG n = 30	1267	25603	5660	19943
ALB n = 30	1737	37200	6852	30348

Fecundity

The cumulative numbers obtained are presented in Table 5. The frequency of oviposition was lower (about 27%) in PIG than in ALB. The production of eggs was inferior (about 31%) in PIG than in ALB. These differences are statistically significant. The absolute numbers of abortive eggs did not differ in PIG and ALB. The hatchability was highly significantly lower in PIG than in ALB. The number of offspring of the first generation is highly significantly lower in PIG than in ALB (about 34%) (Table 6).

The difference between the numbers of eggs per clutch seems to be not very important, but the number of clutches monitored was high (3004) and the difference is in fact highly significant (Table 6). The mean number of eggs per clutch was higher in ALB than in PIG, but the extreme values were not very different: PIG, 1-60; ALB, 1-62.

Table 6. Fecundity of PIG and ALB *Biomphalaria glabrata* rearded separately during 16 weeks. All characteristics of fecundity are compared by the analysis of varience, except the hatchability, which is compared by the chi-square test.

Snails	Clutches/ snail/day	Eggs/snail day	Eggs/clutch	Abortive eggs/ snail/day	Viable eggs/ snail/day	Hatchability
PIG n = 30	0.377 ± 0.019	7.62 ± 0.59	20.20 ± 0.34	1.68 ± 0.28	5.95 ± 0.50	77.89%
ALB n = 30	0.517 ± 0.018	11.07 ± 0.84	21.41 ± 0.24	2.04 ± 0.26	9.03 ± 0.66	81.58%
P	<0.001	<0.05	<0.001	n.s.	<0.01	<0.001

<0.05, <0.01 and 0.001 = statistically significant differences to the level of probability p = 0.05, 0.01 and 0.001, respectively; n.s. = not significantly different.

All the clutches laid by every parent of the same lot can be pooled and then divided into classes (interval width = 5) (Fig. 3). The relative proportions of the numbers of clutches in each class for the two strains can be compared by the chi-square test. Only the classes 1-5, 6-10 and 21-25 were statistically different. In comparision with ALB, PIG presented an excess of small clutches containing 1 to 10 eggs and a significantly reduced number of clutches containing 21 to 25 eggs.

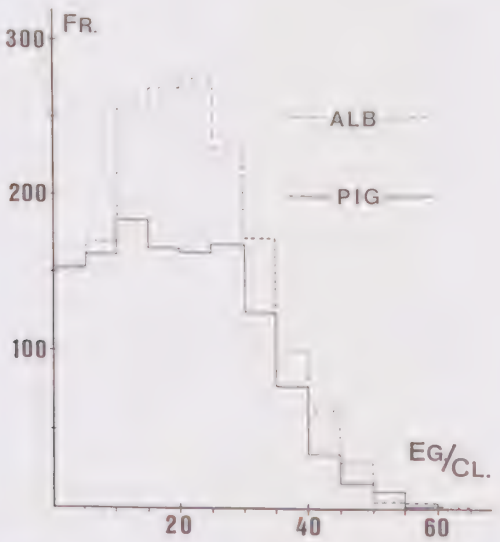

FIG. 3. Histogram of the numbers of eggs per clutch in PIG (n = 1267) and ALB (n = 1737) *Biomphalaria glabrata* egg masses. FR = frequency; E.G./CL = eggs per clutch.

The dry weight of the clutches from the two strains was compared. It appears that the dry weight corresponding to one egg is not statistically different in PIG (4.1×10^{-5}g) and ALB (3.7×10^{-5}g). So, since ALB lays a significantly higher number of eggs, they use a larger quantity of energy for reproduction than does PIG.

DISCUSSION

In *Biomphalaria glabrata*, the genetic control of pigmentation has been studied by Newton (1954, 1955) and by Richards since 1967 (see review in Richards, 1985). Pigmentation often has been used as a genetic marker in experimental studies, but, paradoxically, little attention has been paid to possible differences between PIG and ALB strains' growth or reproduction. In young *B. glabrata*, 30 days after hatching, the shell diameter is similar in pigmented and albino snails, while the weight is significantly higher in albino than in pigmented snails (Chquiloff *et al.*, 1978). Freitas *et al.* (1975) reported growth expressed by the increase of the shell diameter in albino and pigmented snails; it appears that grouped mature snails presented a parallel increase in shell diameter, but probably at a significantly higher level in albino snails.

In my experiments, two homozygous strains, ALB and PIG, were statistically compared. The shell diameter and the body wet weight differed in PIG and ALB from the first week of the experiment, and the PIG were significantly larger and heavier than ALB. These results differ from those shown previously by Freitas *et al.* (1975) and Chquiloff *et al.* (1978). It should be noted that my results concern *Biomphalaria glabrata* reared in isolation throughout the experiment, while the other authors report results from grouped snails. Crowding and the mode of fertilization (selfing in isolated snails, crossing in grouped snails) perhaps explain the differences between my results and those reported by these authors.

It will be interesting to determine if grouping or isolating snails has an influence on the growth of *B. glabrata* of each genotype.

My results show that the comparison of growth curves from various localities should take into consideration the pigmentation of the snails if several genotypes are present in the populations.

In PIG and ALB, the onset of egg laying can be regarded as simultaneous. Nevertheless, an observed variation should be noted: the last PIG reproduced by selfing 41 days after the first ALB. Also, the size and weight of the snails at the onset of egg laying differed statistically. The mean shell diameter and the mean weight were significantly higher in PIG than in ALB. Consequently, the measurement of the size or of the weight of snails is not accurate for determining if snails have or have not reached sexual maturity. For example, it is a common assertion that in *Biomphalaria glabrata* the onset of egg laying occurs for a shell size from 10-11 mm (Brumpt, 1941). Firstly, the mean values are significantly different in PIG and ALB (10.9 and 8.7 mm), and secondly the variation is important: one PIG laid its first clutch at a shell diameter of 13.4 mm, while an ALB was sexually mature at a shell diameter of 6.1 mm.

Scherrer *et al.* (1976) studied the fecundity of four strains of *Biomphalaria glabrata*: pigmented, albino, pigmented and checked, albino and checked. They showed that pigmented and albino strains, studied for 37 days, presented, probably after selfing, a similar fecundity. My results are obviously different, and to the contrary, showed that the fecundity of ALB is significantly higher than in PIG.

The mean numbers of observed clutches per snail per day and eggs per snail per day were less than those reported by Scherrer *et al.* (1976), but are closely related to the numbers available in the literature (see review in Scherrer *et al.*, 1976). The same is true for the number of eggs per egg mass. It is not easy to explain differences between results obtained under various experimental conditions. Nevertheless, in my results, whatever the absolute values obtained, the most striking result is the significant difference between the fecundity of the two homozygous strains ALB and PIG reproducing strictly by selfing.

Richards (1967, 1973) demonstrated that albino snails (without eye pigment) are homozygous cc. On the other hand, pigmented snails present five different phenotypes and genotypes. In my experiments, I previously had isolated a pigmented homozygous strain whose phenotype is CC (black eyes, body, collar and mantle) as defined by Richards (1973). The differences between my results and those of the Brazilian authors may be due to the usage, in their experiments, of various "pigmented" phenotypes and genotypes.

Growth and fecundity differ in ALB and PIG *Biomphalaria glabrata*. Growth is faster in PIG and fecundity is more important in ALB. Snails consume energy for body growth and for reproduction. The ponderal body growth and the weight of clutches show that the PIG use more energy for growth, while ALB use a larger part of the energy for reproduction.

The present results have been obtained in the laboratory. It would be interesting to verify if they are similar in snails living in natural habitats. However that may be, *Biomphalaria glabrata* is a species commonly bred and studied in laboratories. Therefore, the results shown here should indicate caution when biological features such as growth, onset of egg laying or fecundity are recorded

during experimental studies. The experimental results could vary according to the snails' genotypes.

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MARC VIANEY-LIAUD

Laboratoire de Génétique
Institut des Sciences de l'Evolution
U.R.A. - C.N.R.S. 327
Université des Sciences et Techniques du Languedoc
Place Eugène Bataillon
34060 Montpellier, France

Malacological Review, 1989, 22: 33-38

REDESCRIPTION OF TWO NERITES, *SEPTARIA MACROCEPHALA* AND *SEPTARIA SANGUISUGA* (MOLLUSCA: GASTROPODA: NERITOIDEA) FROM THE SOUTH PACIFIC

A. Haynes and E. Wawra

ABSTRACT

The freshwater limpet-like nerite, *Septaria macrocephala* (Le Guillou), which inhabits the fast flowing streams on South Pacific islands, is shown to be two species. Martens mistakenly combined *S. sanguisuga* (Reeve) with *S. macrocephala* in 1881. Differences in shell shape, shell marking, the way in which the shell is eroded, the shape of the opercula and the size and shape of the spermatophores are described and these all point to both *S. macrocephala* and *S. sanguisuga* being distinct species.

INTRODUCTION

The species *Septaria macrocephala* (Le Guillou in Récluz 1841) and *S. sanguisuga* (Reeve 1856) were combined under the older name by Martens (1881), who considered that *Navicella scarebeus* Reeve 1856 and *N. magnifica* Reeve 1856 were also synonyms of *S. macrocephala*. The genus *Septaria* Férussac 1807 predates *Navicella* Lamarck 1809, the name by which the genus has often been known in the past.

The two species have been confused on many occasions. In 1863, Gassies identified specimens from New Caledonia as *Navicella sanguisuga*, but his illustration shows that they were *Septaria macrocephala*. E.A. Smith (1885) identified specimens from Fauro Island, Solomon Islands, as *Neritina sanguisuga*. He described the operculum for the first time, as being narrow with a projection of nearly the same length on each side in front. In describing the terrestrial and freshwater molluscan fauna of New Caledonia, both Crosse (1894) and Franc (1956) were of the opinion that *S. sanguisuga* was a synonym of *S. macrocephala*. Haynes (1984) separated these superficially similar species by the differences in shell and operculum shape. She identified them as *S. macrocephala* and *S. borbonica* (Bory de Saint Vincent 1803) or *S. sanguisuga* in an amended printing (Haynes, 1988).

The aim of this paper is to show that the South Pacific species "*Septaria macrocephala*" of various authors is composed of two separate species. The two species, *Septaria macrocephala* and *S. sanguisuga*, are redescribed and the differences between them are highlighted.

METHODS

The radula, operculum and spermatophores of each species were investigated. The operculum, which is embedded in the ventral muscle, was dissected out and examined under a dissecting microscope. The female spermatophore sacs were opened and the spermatophores were removed and examined. The radula sac, which lies dorsal to the gut and reproductive organs, was opened and the radula was examined by both light microscopy and scanning electron microscopy.

MATERIAL EXAMINED

Septaria macrocephala material examined included: Four syntypes from Museum d'Histoire Naturelle Geneve (NHNG); material of Starmühlner (1976), Naturhistorisches Museum Wien (NHMW No. 7935); five specimens kept at NHMW (No. 84510); 10 specimens from Fiji and two specimens from Samoa collected by Haynes 1984-86, University of the South Pacific (U.S.P.).

Septaria sanguisuga: three syntypes from the Cuming collection at the British Museum (Natural History) (BMNH No. 1974119); three specimens originally identified as *S. macrocephala* (NHMW No. 83431) from Cote Est, New Caledonia collected by Bargibant & Pollabauer in 1982; eight specimens from Fiji, three specimens from New Georgia, Solomon Islands, three specimens from Savai'i, Western Samoa, collected by Haynes during 1984-87, and two specimens from Ponape collected by Maciolek & Ford in 1986.

SYSTEMATIC DESCRIPTIONS

Septaria macrocephala (Le Guillou in Récluz 1841)
(Figs. 1a,b; 3a, 4b)

Navicella macrocephala Le Guillou in Récluz 1841
Navicella sanguisuga, Gassies (1863)
Navicella macrocephala, Martens (1881)

Type: Four syntypes in the Museum d'Histoire Naturelle Geneve.

Type locality: Levuka, Fiji.

Shell: Oblong-ovate, shallowly convex, yellow-brown with black line markings in wavy lines, small diamonds and triangles. Black lines fading with age. Growth lines visible. Inside the shell is bluish and the muscle scars which are obvious on either side disappear under the septum. The septum, which is tinged gold-brown and often has black splashes at either corner, is the widest part of the shell. The large apex, which protrudes beyond the septum, is usually more or less eroded away (Figs. 1a, b).

Operculum: Has one rib projecting forward and the horny portion varies from yellow through orange to black (Fig. 3a).

Spermatophores: Long, thin and cream coloured, 4-5 in each spermatophore sac (Fig. 4b).

Distribution: Nubulevu Creek, Kadavu; Naivika Ck., Taveuni; Naisago and Levuka Cks., Ovalau, Fiji (Haynes, 1988); Le'ele Ck., Tutuila, American Samoa. It has been reported from Tahiti and Vanuatu (Starmühlner, 1976).

Remarks: Three of the type specimens are easily recognized as *Septaria macrocephala*, while the largest one is more deeply convex than most *S. macrocephala*. The diagnostic features given by Riech (1937) for *S. macrocephala*, i.e., the flatly eroded apex and the slanting septum, fit *S. sanguisuga* better than *S. macrocephala*. Starmühlner (1976, figs. 139, 140 & 155) undoubtedly described *S. macrocephala* as the apex of the shell is eroded and the operculum has only one rib projecting forward, but his concept of the species, as seen from his citations, is the same as Martens (1881), i.e., he believed that *S. macrocephala* and *S. sanguisuga* were synonyms.

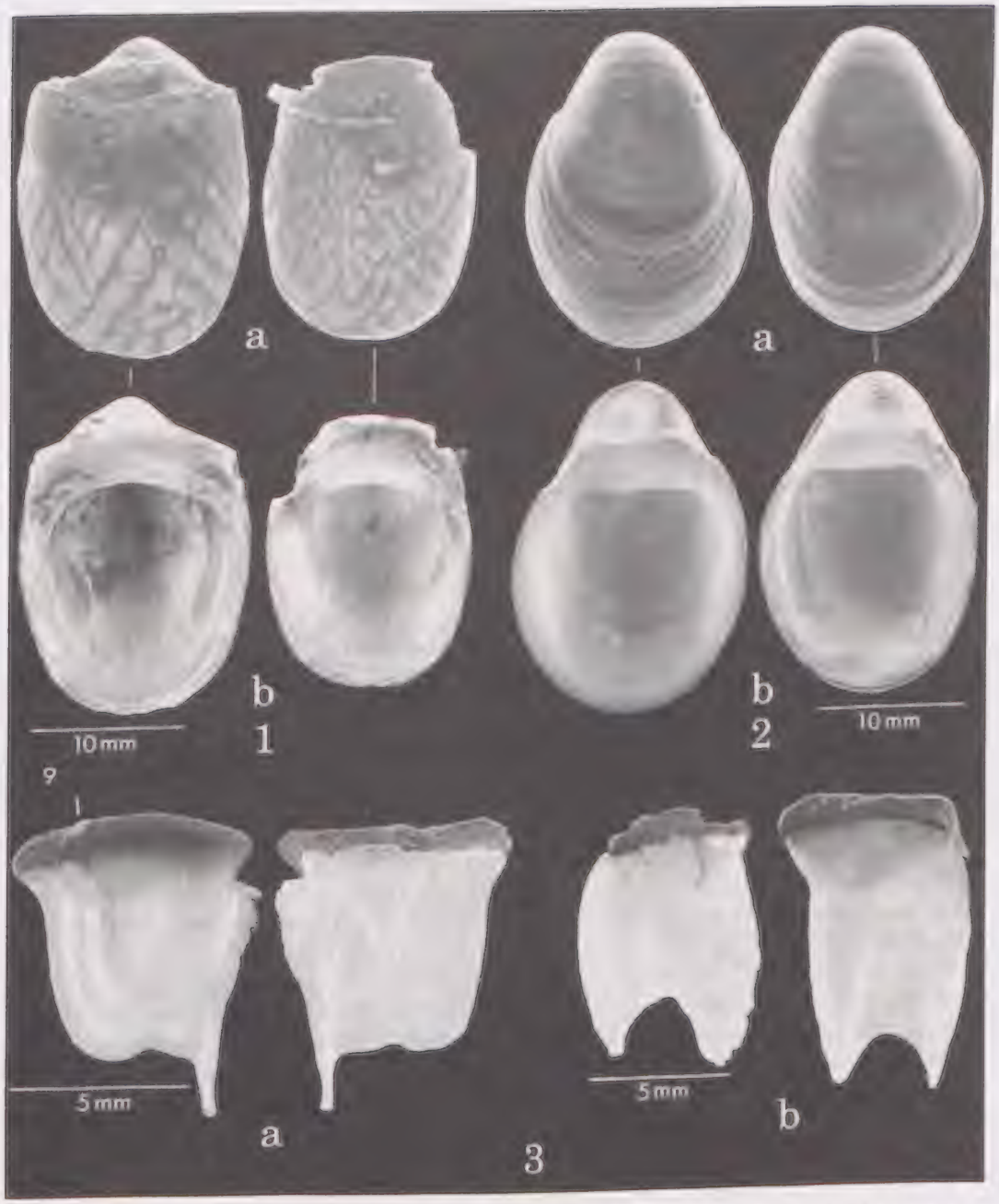

FIG. 1. *Septaria macrocephala* shells; a, Dorsal view; b, ventral view. FIG. 2. *Septaria sanguisuga* shells; a, Dorsal view; b. ventral view. FIG. 3. Opercula; a, *S. macrocephala;* b, *S. sanguisuga.*

FIG. 4. Spermatophores; a, *S. sanguisuga*; b, *S. macrocephala*.

Septaria sanguisuga (Reeve 1856)
(Figs. 2a,b; 3b, 4a)

Navicella sanguisuga Reeve 1856
Navicella macrocephala, Martens (1881)
Neritina sanguisuga, E.A. Smith (1885)
Septaria macrocephala, Riech (1937)

Type: Three syntypes from Cuming collection at British Museum (Natural History) (No. 1974119).

Type locality: New Caledonia.

Shell: Oblong-ovate, deeply convex, brown coloured and sometimes with black wavy lines following the growth ridges which are prominent. Inside the shell is bluish and the sloping septum and apex are orange. The large apex, which erodes horizontally, forms a flat surface across the end. The shell widens below the septum (Figs. 2a, b).

Operculum: Pink with 2 ribs of nearly equal length, projecting forward. The horny area orange (Fig. 3b).

Spermatophores: Thick, solid, bilobed and purple in colour. One spermatophore may extend out of the spermatophore sac and fill the vagina. Two to three discharged spermatophores also in each spermatophore sac (Fig. 4a).

Distribution: Nasekawa R. and Bagasau Ck., Vanua Levu; Naisago and Levuka Cks., Ovalau; Navure Ck., Gau; Nubulevu Ck., Kadavu and Naiviki Ck., Taveuni, Fiji (Haynes, 1988); Vaisigano R., Upolu and Le'ele Ck., Savai'i, Western Samoa; Puha R., New Georgia, Solomon Islands; Upper Nanepil R., Ponape (Maciolek & Ford, 1987); Cote Est, New Caledonia.

Remarks: Unfortunately there are no opercula with the type specimens. However, the shells are recognizable as *Septaria sanguisuga*. Gassies' (1863, pl. VIII, Fig. 12) description and illustration of *Navicella sanguisuga* are of *S. macrocephala*, while *N. macrocephala* of Martens (1881, table 11, fig. 1-4) consists of a mixture of the two species. His fig. 4 is of *S. macrocephala* and his figs. 1-3 are of *S. sanguisuga*.

DISCUSSION

When radulae of *Septaria macrocephala* and *S. sanguisuga* were inspected with a scanning electron microscope no clear difference could be detected. The drawings of the radulae of *S. macrocephala, S. porcellana, S. suffreni* and *S. lineata* in Starmühlner (1976) are similar to one another, suggesting that radula shape is not a helpful diagnostic character within the genus *Septaria*. Female *S. sanguisuga* contained spermatophores from June to December, while spermatophores were found in female *S. macrocephala* from October to December.

When the stomach contents of *Septaria macrocephala* and *S. sanguisuga* collected from a rock face in Naisago Ck., Ovalau, were inspected, they consisted of similar periphyton. This was composed of diatoms (*Synedra* in *S. macrocephala*; *Cymbella* and *Cocconeis* in *S. sanguisuga*), unicellular Chlorophyta (*Coelastrum* in both species), filamentous Rhodophyta (*Lemanea* in both species), angiosperm tissue in *S. macrocephala*, and rock particles. The two species are found together in fast flowing streams attached by their strong muscular foot to the upper side and under surfaces of rocks and boulders in currents of 30-80 cm/sec. *Septaria sanguisuga* is more likely to be found in shade in groups of two to 10, while *S. macrocephala* is usually abundant over a wider area, often in direct sunlight.

ACKNOWLEDGEMENTS

The authors wish to thank the curators of the British Museum of Natural History and of the Museum d'Histoire Naturelle Geneve for allowing us to examine the type specimens of *Septaria sanguisuga* and *S. macrocephala*.

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A. HAYNES

School of Pure and Applied Sciences
University of the South Pacific
P.O. Box 1168
Suva, Fiji

E. WAWRA

Naturhistorisches Museum Wien
Burgring 7, Postfach 41
Vienna, Austria

Malacological Review, 1989, 22: 39-53

ECOLOGICAL STRATEGIES OF HONG KONG THIARIDAE (GASTROPODA: PROSOBRANCHIA)

David Dudgeon

ABSTRACT

Studies of the habitat relations, populations dynamics, growth and reproduction of three Hong Kong Thiaridae, *Thiara scabra*, *Melanoides tuberculata* and *Brotia hainanensis*, have been undertaken. The former two species inhabit slow-flowing or standing waters, but differ in their sediment preferences. They are short-lived (typically < 2 years), and, as only a small proportion of the population survive more than one breeding season, they are essentially semelparous. Both species are parthenogenetic and viviparous, but *M. tuberculata* grows rapidly and is the more fecund. *Thiara scabra* is stenotopic and has poor tolerance of environmental perturbation and desiccation. *Melanoides tuberculata* is relatively tolerant of desiccation and occupies a wide range of habitats, rapidly colonizing areas of new habitat. *Melanoides tuberculata* replaces *T. scabra* at sites experiencing significant water level fluctuations.

Brotia hainanensis is confined to stony hill-streams and the upper course of rivers. It is long-lived (up to 3.5 years) and slow growing, attaining sexual maturity at 2.5 years of age. This species experiences high pre-reproductive mortality and is dioecious. Selection pressure arising from these characteristics has favored iteroparity, large brood size and recruitment of two cohorts of *B. hainanensis* each year.

INTRODUCTION

The family Thiaridae is widespread in tropical Asia (Brandt, 1974), occupying a range of lentic and lotic habitats wherein individual species may comprise a significant proportion of benthic biomass (Dudgeon, 1983a). Also of importance is the role of thiarids as intermediate hosts of parasites of humans and their animals (Abbott, 1952; Davis, 1971; Chaniotis *et al.*, 1980a; Tang, 1985). Notwithstanding, their biology and ecology is poorly known. For example, although these viviparous snails were previously characterized as parthenogenetic (Morrison, 1954), dioecious species of Thiaridae are known (Davis, 1971), and intraspecific variability in sexual expression can occur (Berry & Kadri, 1974; Dudgeon, 1986; *cf.* Livshits & Fishelson, 1983). Even when present, males may not be functional (Chaniotis *et al.*, 1980b).

Three Thiaridae are known from Hong Kong freshwaters: *Melanoides tuberculata* (Müller 1774) and *Thiara scabra* (Müller 1774), which occur in slow-flowing or standing waters (Dudgeon, 1982a; 1983a; 1986; Yipp, 1983), and *Brotia hainanensis* (Brot 1872) which is confined to stony hill-streams (Dudgeon, 1982b; 1983b). The following account of their ecology reviews previous studies of these species in Hong Kong (Dudgeon, 1982a; b; c; d; e; 1983a; b; 1986; Dudgeon & Lam, 1985; Dudgeon & Yipp, 1985), as well as unpublished observations, with a view to elucidating the influence of habitat characteristics on thiarid life history strategies. Strategy as used here is defined as the sum of adaptations of an organism allowing maintenance and reproduction under particular sets of conditions.

MATERIALS AND METHODS

Data on the ecology of Hong Kong thiarids recorded in this paper are based upon studies carried out in Plover Cove Reservoir (September 1978 - June 1979; *Thiara scabra* and *Melanoides tuberculata*), Tai Po Kau Forest Stream (August 1977 - March 1979; *Brotia hainanensis*), and at Ping Long in the Lam Tsuen River Valley (March 1982 - March 1983; *M. tuberculata*), supplemented by observations upon snails maintained in the laboratory. The population dynamics of each species was monitored for at least 13 months, involving sampling at approximately 14-day (*T. scabra* and *B. hainanensis*) or monthly intervals (*M. tuberculata*). Owing to water level fluctuations and the nature of the rocky substrate, quantitative samples on an areal basis could not be obtained for *T. scabra* or *B. hainanensis*. They were sampled by washing stones and cobbles (upon which snails crawled) into a 200 µm mesh net, so that each size group was taken in proportion to its relative abundance in the habitat. *Melanoides tuberculata* were collected by taking 16 0.1 m^2 samples (using a dredge with a net of 200 µm mesh size attached) on each visit to the collecting site. This procedure yielded data on population size-frequency and standing crop, which have been used to calculate production of *M. tuberculata* (Dudgeon 1986). Some data on the population structure and recruitment periods of all three species have been presented elsewhere (Dudgeon, 1982a; b; 1986), but the results presented herein on growth rates have not been published before.

Information upon the reproduction of each species was obtained by decalcifying and dissecting snails of all but the smallest size classes; *i.e.*, those individuals < 3 mm shell width at aperture. Shell aperture was employed as an index of size because dissolution of the spire of larger individuals obviated the use of any other shell dimension. Particular attention was paid to enumerating the contents of the dissected cephalic brood pouch. Data on the sexuality and fecundity of Hong Kong *Thiara scabra* and *Brotia hainanensis* have not been available previously.

RESULTS

Habitat relations

Brotia hainanensis is confined to stony hill-streams and the upper course of rivers in Hong Kong (Dudgeon, 1982b; 1983b). The snails are typically epibenthic on stones although large individuals occasionally burrow in sand. The diet may include periphyton, but allochthonous leaf litter appears to be the main food and marked preferences for certain leaf species (*e.g.* the deciduous Sweet Gum *Liquidambar formosana* Hance: Hammamelidaceae) are exhibited (Dudgeon, 1982e). Foraging patterns are concordant with the hypothesis that the diet of *B. hainanensis* comprises unpredictably and patchily distributed food items (Dudgeon & Lam, 1985).

Large populations of *Thiara scabra* in Hong Kong were previously known only from Plover Cove Reservoir, where the species occurred on both rocky and sandy shores (Dudgeon, 1982a; 1983a) dominating the gastropod community on hard substrata. The snails appeared to graze periphyton and epipsammic algae. Collections from the reservoir in 1983, however, failed to produce living *T. scabra*, and this species may have been eliminated by marked water level fluctuations in Plover Cove since 1978. Such fluctuations may have contributed to the decline of *T. scabra* in two ways: firstly, after stranding by falling water levels these snails have poor tolerance of desiccation. At relative humidities of 60-70%, *T. scabra* survived 14 days (LT_{50} = 12 days) on mud but only three days (LT_{50} = 2 days) in the absence of such substrate (Dudgeon, 1982c). Secondly, falling water levels in Plover Cove expose the rocky marginal zone substratum, forcing *T. scabra* to move onto less-preferred muddy sediments. *Thiara scabra* has poor mobility on fine-grained sediments, and the snails may be smothered by fine particles (< 125 µm grain size; Dudgeon, 1982d). An increased incidence of silt in

Plover Cove sediments accompanies rising water levels (Dudgeon, 1982d; 1983a) and may be a barrier to *T. scabra* recolonizing previously occupied habitat.

Melanoides tuberculata is a widespread inhabitant of slow-flowing or standing waters in Hong Kong, thriving at sites which are mildly enriched by agricultural effluents (Yipp, 1983). The species is also common in Plover Cove Reservoir (Dudgeon, 1983a), where it colonized and temporarily dominated rocky marginal areas following a rise in water levels (Dudgeon, 1982a). *Melanoides tuberculata* is primarily a deposit feeder (Dudgeon & Yipp, 1985), and foraging patterns are concordant with the hypothesis that the snail unselectively ingests fine particles (Dudgeon & Lam, 1985). Dominance of newly-inundated muddy areas of reservoir shore (Dudgeon, 1983a), as well as pools and flooded channels associated with agricultural activities in Hong Kong, reflects the ability of *M. tuberculata* to crawl or burrow through fine sediments (< 125 μm grain size) and aggregate them (Dudgeon, 1982d). As discussed above, such substrates are a barrier to colonization by *T. scabra*. In addition, *M. tuberculata* survives up to 32 days (LT_{50} = 31 days) desiccation on a mud substrate, and 20 days (LT_{50} = 16 days) on bare trays in the absence of mud (Dudgeon, 1982c).

Population dynamics and growth

The population structure of Hong Kong Thiaridae (Fig. 1) exhibits a pattern of progressive loss of individuals in succeeding age classes following a peak in the relative abundance of small snails. That this peak does not coincide with the smallest size group reflects variation in the shell width (at aperture) of hatchlings (in *Thiara scabra* and *Melanoides tuberculata*) as well as differences in the growth rates of animals within each time interval (*Brotia hainanensis*).

As a consequence of their different habitat preferences, interspecific variation in patterns of thiarid mortality could be anticipated. If loss of individuals from a population is age independent, the numbers of animals in succeeding age classes will decline in a negative exponential manner and their logarithms should fall along a straight line. A change in slope (increased steepness) indicates age-dependent loss (Southwood, 1978). Fig. 2 shows $\log_e$ of the total number of live snails of each species plotted against shell width, with a straight line through these points fitted by least mean squares. Against the reference lines, changes in slope become apparent. Survival of young (> 2 mm shell width) *Thiara scabra* and *Melanoides tuberculata* was somewhat better than would be expected from the assumption of age-independent loss but, beyond a certain size (6 mm for *T. scabra* and 9 mm for *M. tuberculata*) age-dependent mortality was high. *Brotia hainanensis* of 3-6 mm shell width experienced lower mortality than their conspecifics; mortality of larger snails was age independent until they exceeded 20 mm shell width.

Similarities in the size of *Thiara scabra* and *Melanoides tuberculata* as indicated by shell width at aperture, were paralleled by shell size - dry weight relationships (Fig. 3). *Brotia hainanensis* juveniles were heavier than comparable individuals (on the basis of shell size) of the other two species until > 6.5 mm shell width, when *M. tuberculata* were the heaviest species. The rate of weight increase with size was lowest in *B. hainanensis*.

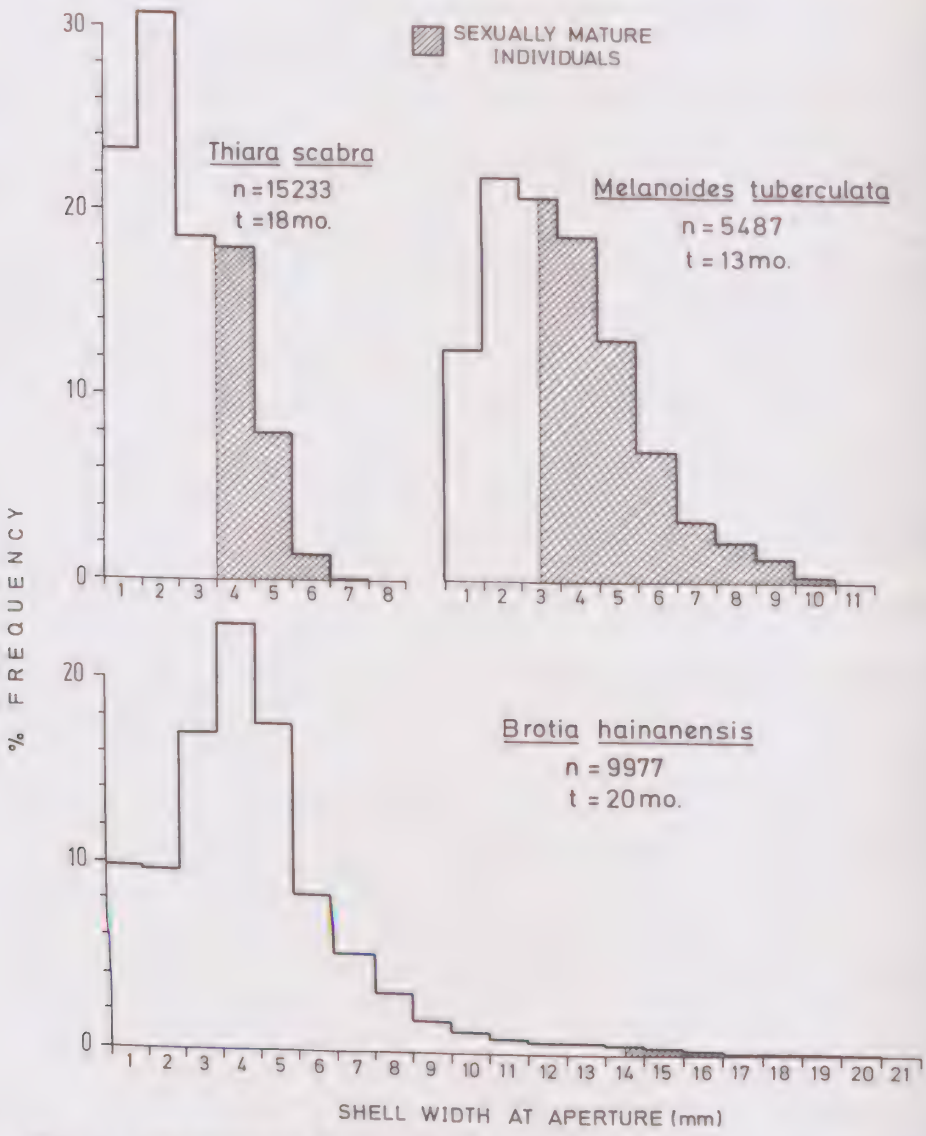


FIG. 1. Size-frequency histograms of Hong Kong Thiaridae collected during investigations of the population dynamics of each species. The proportion of sexually mature individuals in each population and the duration of each study (t) are also shown.

Data on the age structure and juvenile recruitment of Hong Kong thiarids, derived from Dudgeon (1982a; b; 1986), have been reanalysed and are presented in terms of generation composition by month in Figs. 4A, B & C. Over a 12 month period, three generations of *Thiara scabra* could be distinguished in Plover Cove although only two were present at any one time (Fig. 4A). The maximum age of the largest *T. scabra* in the reservoir was therefore little more than two years, although (from Fig. 1) few juveniles lived that long. Juvenile recruitment occurred from September through May, peaking in December and January. Some

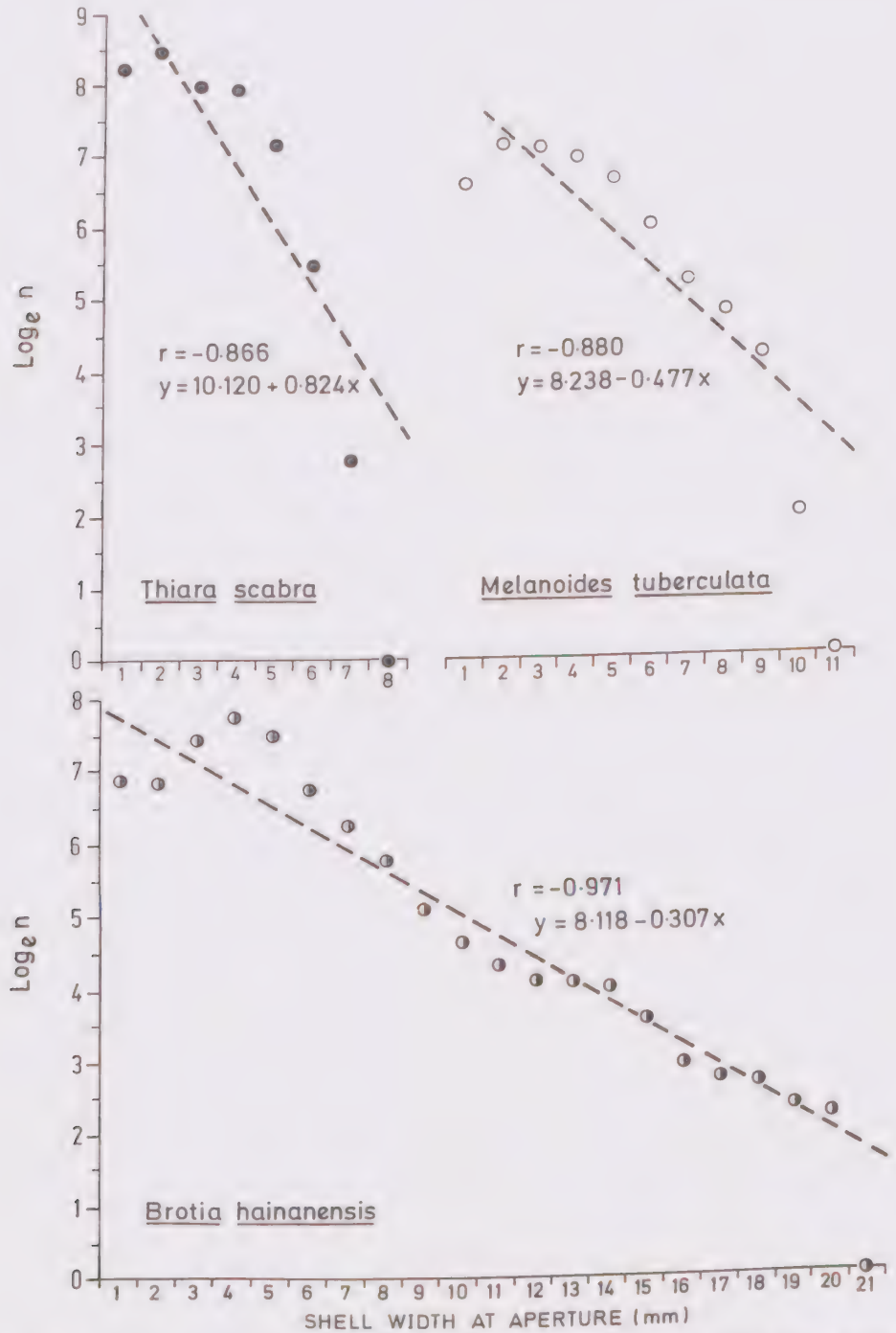


FIG. 2. Log_e total numbers of animals of each size group of three Hong Kong Thiaridae. Best-fitting lines for the relationship between abundance and shell width at aperture for each species is included as a reference against which changes in slope over certain size classes are apparent.

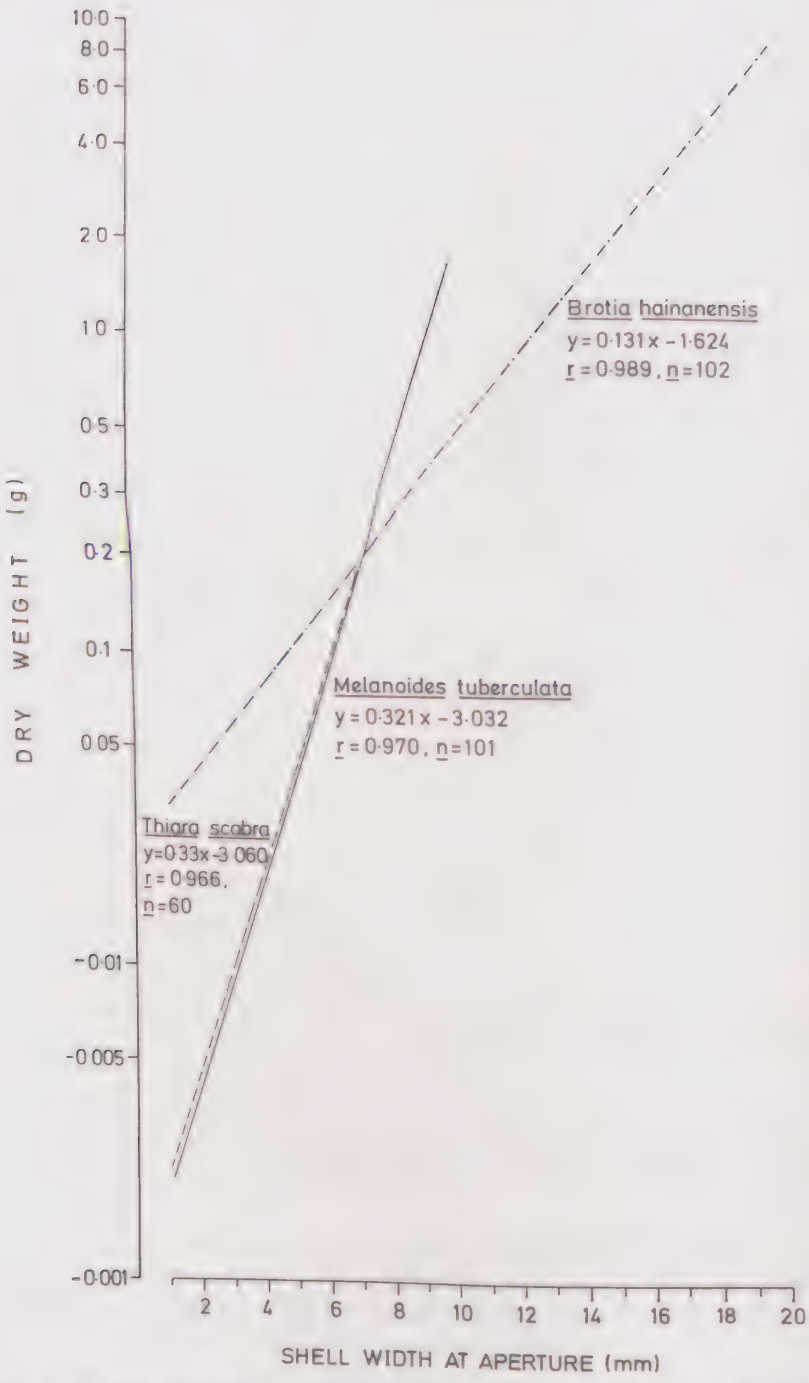


FIG. 3. The relationship between shell width at aperture and dry weight of three Hong Kong Thiaridae. Best-fitting lines were calculated by least mean squares.

individuals apparently survived to breed in two seasons, but most died after breeding once. It is unclear whether repeated breeding (*i.e.*, successive but distinct periods of hatchling release) by an individual within one season is possible.

The monthly generation composition of *Melanoides tuberculata* at Ping Long paralleled that of *Thiara scabra* in Plover Cove, with three generations represented over a 12-month period but only two present at any one time (Fig. 4B). Recruitment took place in summer (June-October), and very few animals survived to breed a second time. The Tai Po Kau *Brotia hainanensis* population had a more complex age structure (Fig. 4C) resulting from a longer life span and the occurrence of two periods of recruitment each year. A first recruitment episode in April and May was followed by a second extending through late July, August and early September. A few hatchlings were also recorded in November. Both the early and late summer cohorts of the current year and those of the previous year were separable, but these cohorts could not be distinguished in two or three year old snails. The maximum life span of *B. hainanensis* was approximately 3.5 years, but animals less than two years old comprised over 90% of the population.

Growth (as indicated by changes in mean shell width for each generation/cohort) continued throughout the year with no evidence of seasonal interruption (Figs. 5A, B & C). Year groups (but not cohorts) remained largely distinct, as indicated by the low overlap in standard deviations of mean shell width between successive generations.

To facilitate inter- and intraspecific comparisons of growth rates, Instantaneous Growth Rates (IGR) of generations/cohorts were calculated according to Bagenal & Tesch (1978) where

$$IGR = \frac{\log_e W_2 - \log_e W_1}{\triangle t}$$

i.e., the IGR is the natural logarithm of the ratio of final weight of the snail in unit time. $\log_e W_1$ and W_2 were derived from Fig. 5 (A-C) by calculating the dry weights of each generation/cohort from the mean shell widths at the beginning and the end of each growth period, using the size-weight relationships given in Fig. 3. *Melanoides tuberculata* had the fastest growth rates of the Hong Kong thiarids (Fig. 6) while those of *Brotia hainanensis* were the slowest. IGR declined with age so that the youngest snails of each species had the fastest growth rates, while the oldest snails grew the slowest.

Sexuality and reproduction

Melanoides tuberculata were sexually mature at 3.5 mm shell width, while *Thiara scabra* attained maturity at 4.0 mm shell width. By contrast, *Brotia hainanensis* did not mature until a shell width of 14.5 mm (Fig. 1). Consequently, *M. tuberculata* had the highest proportion of sexually active individuals in the population, while *B. hainanensis* had the smallest (Fig. 1).

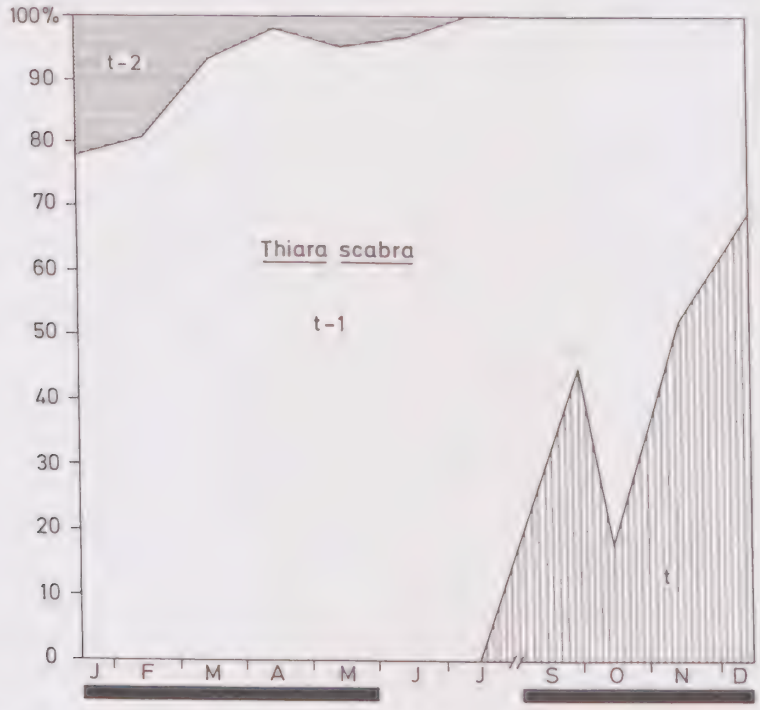


FIG. 4A. *Thiara scabra*: generation composition by month of the Plover Cove Reservoir population, where t = generation 0, t-1 = generation 1, and t-2 = generation 2.

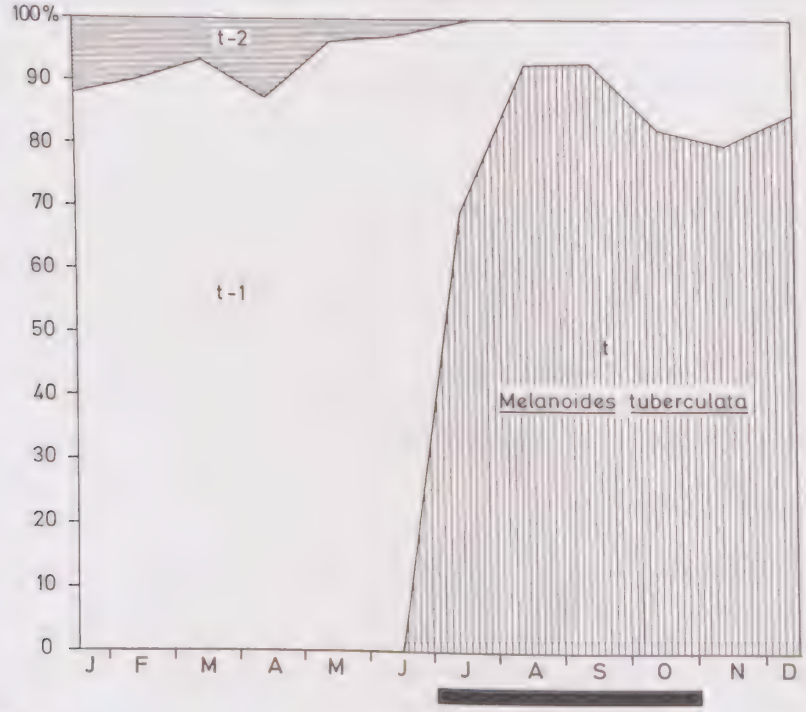


FIG. 4B. *Melanoides tuberculata*: generation composition by month of the Ping Long population, where t = generation 0, t-1 = generation 1, and t-2 = generation 2.

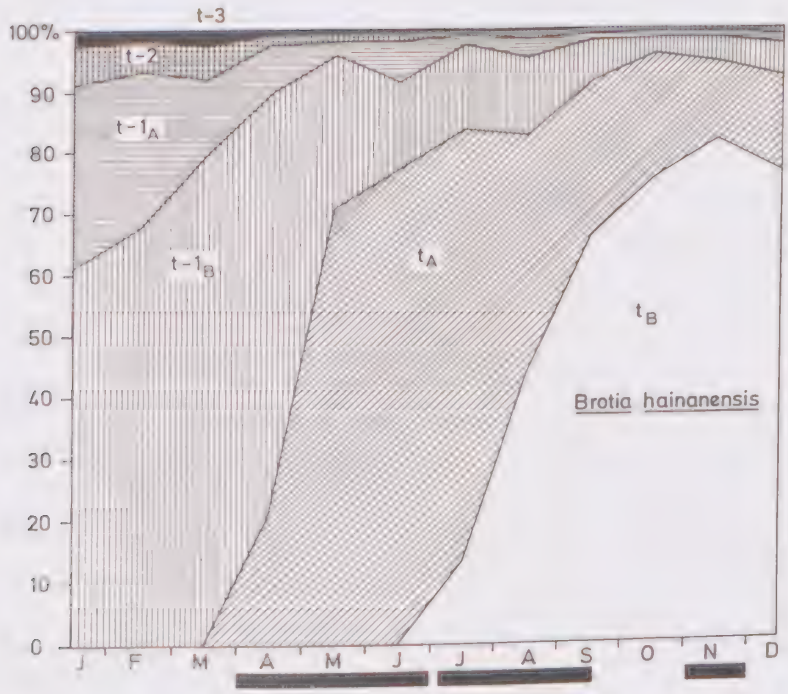


FIG. 4C. *Brotia hainanensis*: generation/cohort composition by month of the Tai Po Kau Forest Stream population, where t_A = generation 0 (first cohort), t_B = generation 0 (second cohort), $t\text{-}1_A$ = generation 1 (first cohort), $t\text{-}1_B$ = generation 1 (second cohort), t-2 = generation 2, and t-3 = generation 3.

Hong Kong *Melanoides tuberculata* and *Thiara scabra* were parthenogenetic, as has been recorded for these genera elsewhere (Abbott, 1952; Berry & Kadri, 1974; Brandt, 1974; Chaniotis *et al.* 1980b; Stoddard, 1983). All sexually mature individuals had brood pouches and were therefore female. However, not all functional females had young in the brood pouch, although eggs as well as fully-formed young were recorded from *M. tuberculata* brood pouches throughout the year (Dudgeon, 1986). Unfortunately, no data on seasonality of egg production by *T. scabra* or *B. hainanensis* are available (brood pouch samples for these species were collected in June and April respectively).

It seems clear that *Brotia hainanensis* is not parthenogenetic as (of 72 animals dissected) 42% of sexually mature individuals (> 14.5 mm shell width) did not have a brood pouch. Davis (1971) has reported dioecious species in the genus *Brotia* from Malaysia and the Philippines, noting that the prediction of sex from anatomical features was possible even when the females had no embryos (16% of mature Hong Kong *B. hainanensis*).

The brood size of Hong Kong Thiaridae showed considerable inter- and intraspecific variation. Log_{10} brood size was positively related to the shell width of sexually mature *Thiara scabra* and *Melanoides tuberculata* ($r = 0.650$, $n = 28$, $P < 0.001$ and $r = 0.877$, $n = 390$, $P < 0.001$), but this was not the case for *Brotia hainanensis* ($r = 0.361$, $n = 11$, $P > 0.05$) (Fig. 7) reflecting the proportion of females with empty brood pouches. The number of eggs and young per brood pouch varied from 112-936 (maximum number of fully-formed hatchlings = 871) in

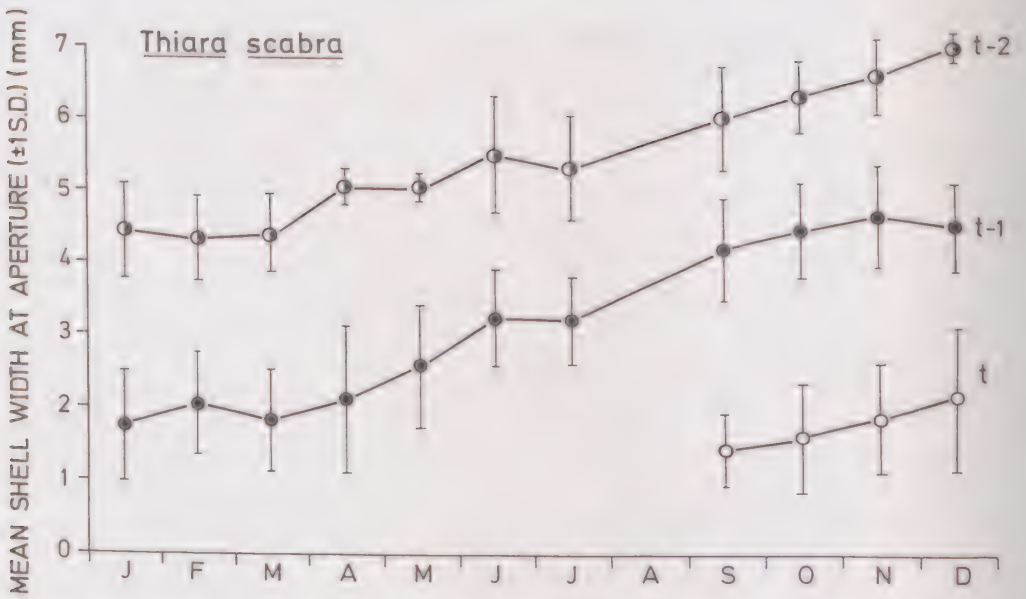


FIG. 5A. *Thiara scabra*: growth rates of each generation of the Plover Cove Reservoir population over a year, as indicated by changes in mean shell width. For abbreviations, refer to Fig. 4A.

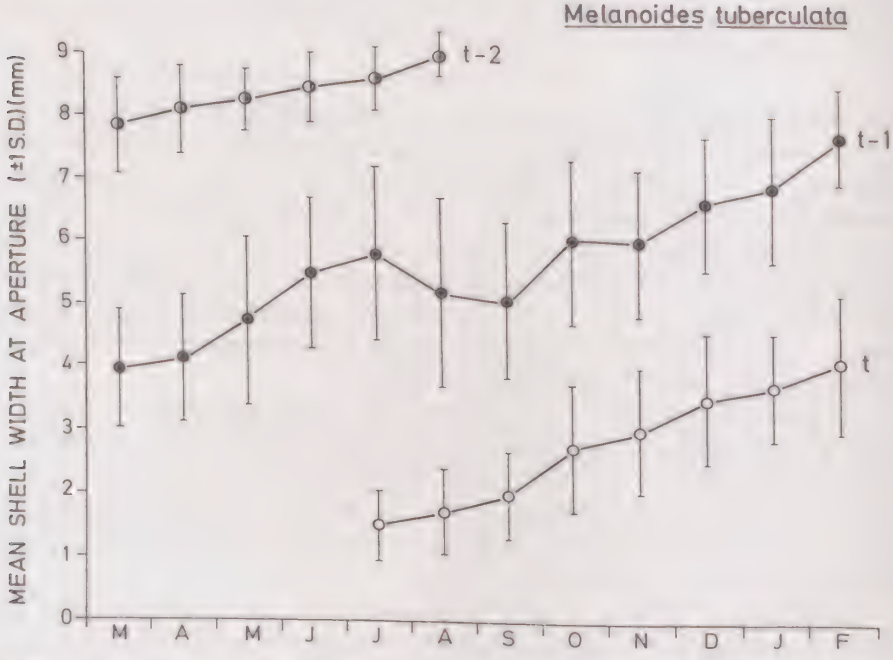
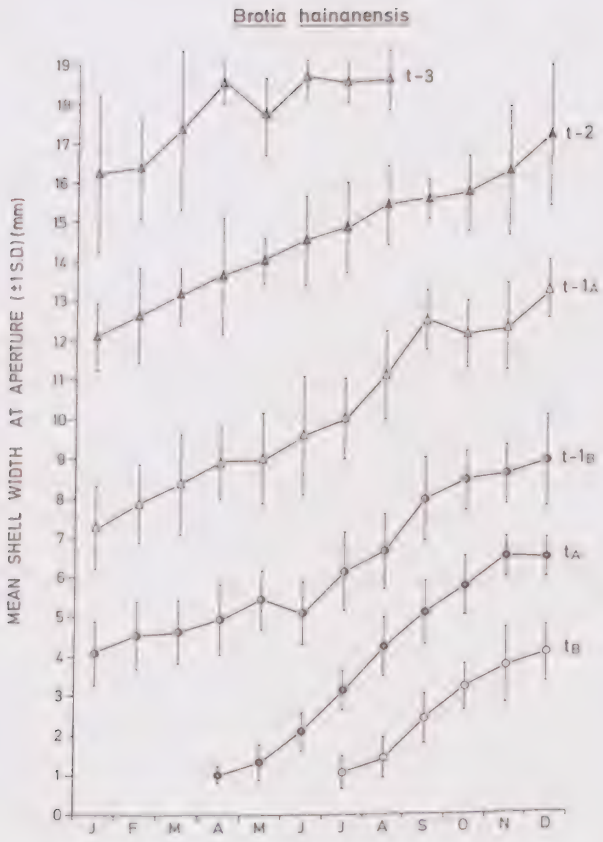


FIG. 5B. *Melanoides tuberculata*: growth rates of each generation of the Ping Long population over a year, as indicated by changes in mean shell width. For abbreviations, refer to Fig. 4B.



5C. *Brotia hainanensis*: growth rates of each cohort/generation of the Tai Po Kau Forest Stream population over a year, as indicated by changes in mean shell width. For abbreviations, refer to Fig. 4C.

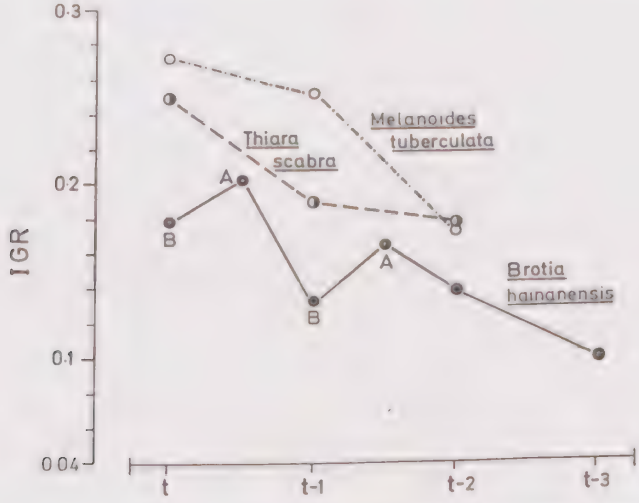


FIG. 6. Instantaneous growth rates (time unit = 1 month) of the generations/cohorts of three Hong Kong Thiaridae, where t = generation 0, t-1 = generation 1, t-2 = generation 2, t-3 = generation 3, and A and B refer to the early and late summer cohorts (respectively) of *Brotia hainanensis*.

B. hainanensis, 5-76 (maximum number of fully-formed hatchlings = 2) in *T. scabra*, and 13-597 (maximum number of fully-formed hatchlings = 6) in *M. tuberculata*. The relatively small proportion of fully-formed hatchlings in *T. scabra* and *M. tuberculata* (which may be a consequence of parthenogenicity) is indicative of an extended period of hatchling release, in contrast to the synchronized development and release of many *B. hainanensis* hatchlings.

DISCUSSION

The Hong Kong Thiaridae show clear evidence of divergence in habitat relations, both at the macrospatial level (running vs. standing waters) and at the microspatial level (within Plover Cove Reservoir). The latter is exemplified by the differential responses of *Thiara scabra* and *Melanoides tuberculata* to fine-grained sediments in Plover Cove. Indeed, the successful exploitation of man-made agricultural habitats by *M. tuberculata* can probably be attributed, in part, to a preference for mud and silt substrata. Compared with *Brotia hainanensis* and *T. scabra*, *M. tuberculata* is highly eurytopic and within Plover Cove is a

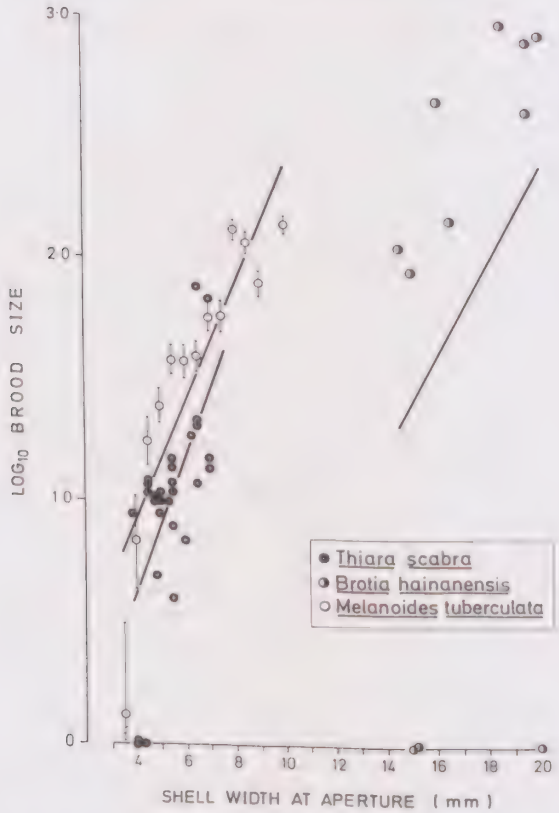


FIG. 7. Brood size in relation to shell width of three Hong Kong Thiaridae. The position of the "best-fitting" line for *B. hainanensis* was strongly influenced by females with empty brood pouches.

speedy colonizer of newly-inundated marginal zone habitat. This exploitation strategy is facilitated by (1) good tolerance of desiccation which enables the snail to survive in habitats which may dry out periodically; (2) rapid growth to sexual maturity; and (3) a greater fecundity than comparably-sized *T. scabra*. Hong Kong *M. tuberculata* exhibit a midsummer peak in juvenile recruitment but rarely attain a large size, few adults surviving to breed in a second season. This species can be regarded as essentially semelparous with a small proportion of iteroparous individuals. Parthenogenicity, rapid growth and a high reproductive investment relative to body size (*i.e.* the ratio of brood mass to body mass) are characteristics of *r*-selected species, and together bestow the ability to colonize rapidly and exploit those habitats which may be only transiently favourable. In combination, the ecological strategies of Hong Kong *M. tuberculata* can be viewed as more typical of a fugitive species (*sensu* Hutchinson, 1951) rather than those of an equilibrium species.

Plover Cove *Thiara scabra* have, by contrast with *Melanoides tuberculata*, narrow habitat requirements and poor tolerance of desiccation. Consequently, the population size of this species is profoundly influenced by water level fluctuations, to the extent that, following inundation by rising waters, habitat previously dominated by *T. scabra* is occupied by *M. tuberculata*. Although *T. scabra* is parthenogenetic, it is less fecund than *M. tuberculata* and therefore has poorer ability to recover from events which reduce population size. *Thiara scabra* is evidently an equilibrium species which can maintain large populations on hard substrata in lentic habitats only in the absence of environmental perturbations (especially water level fluctuations). Where water levels fluctuate and sediment characteristics are suboptimal, *T. scabra* is replaced by *M. tuberculata*.

Brotia hainanensis differs from *Thiara scabra* and *Melanoides tuberculata* in terms of habitat occupation and reproductive strategy. It is the only snail inhabiting stony hill-streams and the upper course of rivers in Hong Kong, and so is unaffected by interactions with other thiarids. Conditions in *B. hainanensis* habitats are predictable from year to year although unpredictable within years according to the extent and duration of spates brought about by the summer monsoon. As a stenotopic inhabitant of lotic habitats, *B. hainanensis* can be considered to be an equilibrium species.

Unlike other Hong Kong Thiaridae, *Brotia hainanensis* is dioecious and grows relatively slowly, attaining maturity when approximately 2.5 years old (14.5 mm shell width). Over 90% of all *B. hainanensis* die before reaching maturity. In compensation for separate sexes (*cf.* the advantages of not producing males; Maynard Smith, 1978) and delayed reproduction, females are highly fecund and may release > 800 hatchlings at one time. Moreover, two distinct annual peaks of hatchling release have been recorded, one preceding and a second immediately following the stream spates associated with the summer monsoon. In this stenotopic species, iteroparity and high fecundity may have evolved as compensation for high pre-reproductive mortality and the possession of separate sexes.

Conventional explanation of an ecological phenomenon commonly relies on showing how the behaviour of an organism is "just right" to enable us to account for its distribution (Harper, 1980). After examination of the whole gamut of a

species' behaviour (form, reproduction, desiccation tolerance, etc.) it can usually be concluded that a species behaves just right for the environment in which we find it (= Panglossian ecology). However, there are two sides to the idea that organisms are suited to their environments: firstly, what is it about them that fits them to those habitats; and secondly, what hinders their living elsewhere?

With reference to the present discussion, it seems clear that the ancestral thiarid stock had separate sexes (*i.e.* was gonochoristic) (Livshits & Fishelson, 1983), and this feature has persisted in the genus *Brotia*. In view of the restriction of *Brotia hainanensis* to environments which parthenogenetic thiarids have yet to colonize, the present distribution of this species may reflect a progressive upstream displacement in habitat as a consequence of interactions with eurytopic and parthenogenetic species (*e.g. Melanoides tuberculata*) possessing good colonizing ability. Testing of such an hypothesis must, however, await further studies of the ecology of Asian Thiaridae.

ACKNOWLEDGEMENTS

The author is grateful to Paul K.S. Lam, Donald J. Macintosh and May W. Yipp for constructive comments on the manuscript. A version of this paper was presented at the 9th International Malacological Congress in Edinburgh (1986).

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DAVID DUDGEON

Department of Zoology
The University of Hong Kong
Hong Kong

Malacological Review, 1989, 22: 55-60

HISTORICAL CHANGES IN THE MUSSEL FAUNA (BIVALVIA: UNIONOIDEA) OF THE STONES RIVER, TENNESSEE

John E. Schmidt, R. Don Estes and Mark E. Gordon

ABSTRACT

Prior to the impoundment of the lower Stones River in 1968, 48 species of unionoid mussels were known from its drainage basin. Thirty-nine stations were sampled upstream from the present reservoir between April, 1980 and March, 1981. Thirty species, including two previously unreported species, were collected. Compared to historical records, these data represent a 40% decline in the river's known fauna and a 25% loss of species within the portion of the river not inundated by the reservoir. Environmental perturbations, such as water quality degradation and illegal gravel dredging, appear to be significant causal factors in the reduction of species diversity within the upper Stones River.

INTRODUCTION

Prior to its impoundment behind J. Percy Priest Dam in 1968, the Stones River supported a diverse assemblage of freshwater mussels, including a significant component of endemic Cumberlandian species. Although Wilson & Clark (1914) collected only 15 species, they considered this river to represent an important tributary source for commercially valuable species within the Cumberland River system. Stansbery (personal communication) recorded 45 species from the Stones River basin between 1965 and 1968. These historical records included two species which were described originally from the Stones River: the presumably extinct *Epioblasma lenior* (Lea 1842) and *E. walkeri* (Wilson & Clark 1914), now federally-designated as endangered. A total of 48 unionid species previously have been reported from the drainage basin. Incidental collecting since the inundation of the lower portion of the river indicated probable reductions in species richness and abundance upstream from the reservoir. With respect to these observations, an intensive sampling program was initiated to determine if changes in species composition had occurred and to examine possible causes for such changes.

STUDY AREA

The Stones River is a major tributary of the Cumberland River in central Tennessee. Its drainage basin incorporates 3021 km^2 (approximately 80% rural) (Schmidt, 1982) and includes portions of Cannon, Davidson, Rutherford, and Wilson counties. J. Percy Priest Dam is located 11 km upstream from the confluence with the Cumberland River and inundates approximately 73 km of the Stones River. Above the reservoir, the upper basin is drained primarily by three main forks of the river. This portion of the drainage lies within the north-central section of the Nashville Basin physiographic region and is geologically dominated by a 150 m thick bed of Ordovician limestone.

MATERIALS AND METHODS

Thirty-nine stations (Fig. 1) were sampled for mussels between April, 1980 and March, 1981. Stations were distributed among the three main forks above the reservoir and were visited two to four times during the sampling period. Mussels were collected by grubbing, searching shallow sections with a viewing bucket, and raking areas of finer particle substrate with a dip-net drag. Species identifications were verified by Drs. D.H. Stansbery, Ohio State University and P.W. Parmalee, University of Tennessee. Voucher specimens were deposited in the Ohio State University Museum.

FIG. 1. Map of Stones River system showing locations of sampling stations.

RESULTS

Thirty species of unionoid mussels were collected from 21 of the 39 sampling stations (Table 1). The East Fork, largest of the tributaries, supported 29 of these species, while 17 species were recovered from the West Fork. Only five species were found in the relatively small Middle Fork. *Villosa taeniata* (Conrad 1834) and *Lasmigona costata* (Rafinesque 1820) were the most abundant and widely distributed species encountered, occurring at 18 and 12 of the sampling sites, respectively. Other species occasionally were abundant locally but were not as widely dispersed as the previous two. Prior to this investigation (Schmidt, 1982), *Alasmidonta viridis* (Rafinesque 1820) and *Villosa vanuxemii* (Lea 1858) had not been reported from this drainage basin. No federally-designated endangered species were encountered.

DISCUSSION

Of the 50 species of mussels known to have inhabited the Stones River system, *Obovaria olivaria* (Rafinesque 1820), *Epioblasma arcaeformis* (Lea 1831), and *E. florentina* (Lea 1857: assuming that this species and *E. walkeri* are distinct) apparently were extirpated prior to Stansbery's collecting. Since 1968, 17 additional species have been lost. Seven of these formerly occupied habitats now inundated. Within the present study area, 10 previously reported species were not recovered. These data indicate a 25% reduction in species richness for the upper river basin and a 40% faunal decline overall since impoundment.

The most obvious disturbance within the Stones River basin has been the construction of the J. Percy Priest Reservoir. This alone has caused an apparent 15% faunal loss due to habitat destruction. However, the extirpation of species upstream from the reservoir illustrates that significant, deleterious environmental impacts have not been restricted only to the lower portion of the basin. Although some environmentally adverse effects upon the upper drainage basin may be attributed to impoundment (*e.g.*, restriction of upstream movements of potential glochidial-host fish: see Harshbarger & Porter, 1982), the observed decline in the above-reservoir mussel fauna probably resulted from locally-derived perturbations.

Physico-chemical data collected during the same period as this study suggested declining water quality (Schmidt, 1982). Mean values for alkalinity (140 mg $CaCO_3/1$), hardness (156 mg $CaCO_3/1$), and pH (7.7) were relatively lower than data presented by Burchett and Moore (1971: 240 mg $CaCO_3/1$, 217 mg $CaCO_3/1$ and 8.0, respectively), indicating possible degradation within the system. Sewage treatment plants at Woodbury, on the East Fork, and Murfreesboro, on the West Fork, have been frequently in violation of state standards for dissolved oxygen (DO) concentrations (Schmidt, 1982). During this study, levels as low as 2.9 mg $0_2/1$ were observed. Depressed DO and associated high BOD (biological oxygen demand), indicative of eutrophication, have been implicated as the cause of numerous fish kills in the upper Stones River basin (Burdick & Drewry, 1973; Tennessee Wildlife Resources Agency, unpublished data). Increased regional agricultural activities (Ashburn, personal communication) also have contributed to eutrophication, siltation, and contamination from pesticides and fertilizers. Persistently low DO and potentially toxic effects related to effluent discharges (*e.g.*, elevated nitrate levels, pesticides) more than likely have contributed significantly to the decline in mussel populations (see Fuller, 1974).

Considerable physical disruption of the river bed has resulted from unauthorized gravel dredging. Nine such activities were reported for the upper Stones River system between 1977 and 1980, but it has been estimated that these reports represented only 1/3 of the actual operations (Martinez, personal communication). Dredging has been documented to destroy habitat and cause deleterious siltation for considerable distances downstream (Ellis, 1931; Cordone & Pennoyer, 1960; Krumholz, *et al.* 1970; Imlay, 1972; Fuller, 1974; Yokley, 1976). At non-lethal sedimentation rates, growth of mussels may be retarded by increased siltation (Stansbery, 1970; Yokley, 1976). The period required by mussels to recolonize dredged areas may be quite prolonged (Yokley, 1976).

It is evident that the mussel fauna of the Stones River system has been heavily impacted by human activities within the drainage basin. No one causal factor may be associated with the decline in diversity, but available habitat presently is quite restricted relative to historical distributions. The upper Stones River today is essentially a closed basin faunally due to the downstream presence of J. Percy Priest Reservoir. This impoundment functions as a physical barrier to upstream movement of glochidial-host fish from outside the Stones River drainage. Natural recruitment from exogenous downstream sources is no longer possible; therefore, potential catastrophic events in the basin could cause faunal extirpation with little chance for recovery. Conditions within the Stones River are representative of many rivers in North America. Continued existence of

Table 1. Historical and distributional synopsis of freshwater mussels from the Stones River, Tennessee (E = East Fork, W = West Fork, B = East and West Forks, A = abundant, R = rare, X = present).

Species	WC[1]	S[2]	Present study/stations																			
			East Fork									Middle Fork								West Fork			
			2	3	5	6	8	9	13	14	16	1	2	3	4	5	6	7	8	2	3	4	5
Cumberlandia monodonta (Say, 1829)		X																					
Fusconaia flava (Rafinesque, 1820)	E	X	A				R	R															
Quadrula pustulosa (Lea, 1831)		X																					
Quadrula quadrula (Rafinesque, 1820)		X																					
Quadrula cylindrica (Say), 1817)		X	R			R																	
Tritogonia verrucosa (Rafinesque, 1820)		X	A	A		X																	
Amblema plicata (Say, 1817)	B	X	A	A	A	A	R					R				R							
Megalonaias nervosa (Rafinesque, 1820)		X	A	A																			
Cyclonaias tuberculata (Rafinesque, 1820		X	A	A								A											
Pleurobema coccineum (Conrad, 1836)		X																					
Pleurobema cordatum (Rafinesque, 1820)		X																					
Pleurobema rubrum (Rafinesque, 1820)		X																					
Pleurobema oviforme (Conrad, 1834)[3]		X	R									R											
Elliptio dilatatus (Rafinesque, 1820)		X	A	A	A	A	A	A				A											
Ptychobranchus fasciolaris (Rafinesque, 1820)		X	R	R																			
Obliquaria reflexa Rafinesque, 1820		X		R																			
Obovaria olivaria (Rafinesque, 1820)	E																						
Obovaria subrotunda (Rafinesque, 1820)	E	X		A																			
Actinonaias ligamentina (Lamarck, 1819)		X																					
Actinonaias pectorosa (Conrad, 1834)[3]		X	R																				
Ellipsaria lineolata (Rafinesque, 1820)		X																					
Truncilla truncata Rafinesque, 1820		X	A																A				
Truncilla donaciformis (Lea, 1828)		X																					
Leptodea fragilis (Rafinesque, 1820)		X	R																				
Proptera alata (Say, 1817)		X		A								A											
Toxolasma parvum (Barnes, 1823)	E	X																					
Toxolasma lividum (Rafinesque, 1831)	B	X	R					R								R		R		R		R	
Medionidus conradicus (Lea, 1834)[3]	E	X	R					R			R					R							R
Ligumia recta (Lamarck, 1819)		X																					

Table 1. (Continued)

Species	WC[1]	S[2]	Present study/stations																			
			East Fork									Middle Fork								West Fork			
			2	3	5	6	8	9	13	14	16	1	2	3	4	5	6	7	8	2	3	4	5
Villosa iris (Lea, 1830)		X	R																				
Villosa taeniata (Conrad, 1834)[3]	W	X	A	A	A	A	A	A	A	A	A	A		A	A	A	A	A		A	A		
Villosa vanuxemii (Lea, 1858)[3]							R	R				R				R							
Villosa lienosa (Conrad, 1834)	E	X	R									R											
Lampsilis teres (Rafinesque, 1820)		X																					
Lampsilis ovata (Say, 1817)		X	R	X	R	R	X	X	X														
Lampsilis ventricosa (Barnes, 1823)	E	X	A	A	X	R	X	X															
Lampsilis fasciola (Rafinesque, 1820)	B	X	A		R	R	A	A	A	R													
Epioblasma arcaeformis (Lea, 1831)[3,4]																							
Epioblasma brevidens (Lea, 1834)[3]		X																					
Epioblasma florentina (Lea, 1857)[3,4]																							
Epioblasma lenior (Lea, 1842)[3]		X																					
Epioblasma walkeri (Wilson & Clark, 1914)[3]	E	X																					
Lasmigona costata (Rafinesque, 1820)	B	X	A	A	A	A	A	A	X			A	R	A	X	R							
Lasmigona complanata (Barnes, 1823)		X	A	A										R		R							
Pegias fabula (Lea, 1836)[3]		X																					
Alasmidonta viridis (Rafinesque, 1820)																		R					
Anodonta imbecillis Say, 1829	B	X	R																			R	
Anodonta grandis Say, 1829	B	X	A									A				A		X				A	
Simpsonaias ambigua (Say, 1825)		X																					
Strophitus undulatus (Say, 1817)	X		R									R											

[1]Wilson & Clark (1914)

[2]Stansbery (unpublished data).

[3]Cumberlandian endemic.

[4]Included in Stones River fauna by Starnes & Bogan (1988). Origins of records not given.

disturbance-sensitive organism, such as unionoid mussels, indicates continued acceptable water quality within a system. Accordingly, activities within drainage basins should be manages to preserve such resources.

ACKNOWLEDGEMENTS

The Tennessee Cooperative Fishery Research Unit is jointly supported by the U.S. Fish and Wildlife Service, Tennessee Technological University, and the Tennessee Wildlife Resources Agency. Funding for this project was provided by the U.S. Army Corps of Engineers, Nashville District. We would like to thank the following for their comments and assistance: E. Ashburn and P.W. Parmalee, University of Tennessee; P.W. Bettoli, Tennessee Technological University; G.J. Martinez, U.S. Army Corps of Engineers, Nashville District; and D.H. Stansbery, Ohio State University.

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JOHN E. SCHMIDT

Ecological Services
U.S. Fish and Wildlife Service
U.S.D.A. Forestry Bldg., Rm. 311
P. O. Box 1278
Elkins, West Virginia 26241, U.S.A.

R. DON ESTES & MARK E. GORDON

Tennessee Cooperative Fishery Research Unit
Department of Biology
P. O. Box 5114
Tennessee Technological University
Cookeville, Tennessee 38505, U.S.A.

Malacological Review, 1989, 22: 61-63

BRIEF COMMUNICATIONS

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TEST OF TELEMETRY TECHNIQUES ON FRESHWATER MUSSELS. - Richard J. Neves, Fred Servello and Rebecca Wajda - Biotelemetry has become an important research tool in aquatic environments, especially for studying the movements of fishes in large lakes and rivers (Winter, 1983). The technique has been used far less frequently on invertebrates -- primarily on marine crustaceans (Lund & Lockwood, 1970; Clifton *et al.*, 1970; Monan & Thorne, 1973; Kanciruk & Herrnkind, 1978; Jernakoff, 1987) and large land snails (Auffenberg, 1982). The application of bio-electronic technology to freshwater bivalves has not been reported, but now the availability of miniature transmitters makes such studies possible on mollusks.

We attempted to evaluate the suitability of magnetometry and radiotelemetry to relocate freshwater mussels (Unionidae) in anticipation of the translocation of endangered mussels, as specified in recovery plans, to historic habitat (Neves *et al.*, 1987). Of the two techniques tested, one proved potentially effective for the remote monitoring of bivalves.

Methods. Magnetometry. A model DM22 portable magnetometer (Dowty RFL Industries, Boonton, NJ[1]) was used to locate specimens of the mucket, *Actinonaias ligamentina* (Lamarck 1819) that had been placed at marked locations in the New River, western Virginia. The magnetometer, consisting of a control box and hand-held ring-core fluxgate sensor (probe), measures magnetic field intensity or differential, indicated by a bipolar meter and audible tone. Magnetic fields ranging from ± 10 Gamma to ± 100,000 Gamma can be measured by using one of seven full-scale ranges of sensitivity.

Disk magnets of three strengths (3.5, 18, 27 million GaussOersted) and two diameters (8.4 and 12.7 mm) per strength were attached, one to each mussel. The magnets were secured externally, dorsad to the posterior ridge, with waterproof epoxy. Tagged specimens of *A. ligamentina*, 80-120 mm long, were pushed into the river bottom at known locations. We then conducted a systematic search for these attached magnets (mussels) by sweeping motions of parallel arcs within 5 cm of the substratum as we waded in the river. The deflection of the gamma meter needle indicated proximity to a magnet. As the probe passed over or near the magnet, needle deflection changed from one end of the scale to the other, reflecting the opposite poles of the magnet. Preliminary field tests were conducted to assess background magnetism and the appropriate sensitivity level to set the magnetometer. To prevent false readings, we used a sensitivity scale that would ensure that background levels of magnetism did not exceed one-half scale deviation.

Radiotelemetry. Radio transmitters purchased from two companies (Advanced Telemetry Systems, Bethel, Minnesota; L.L. Electronics, Mahomet, Illinois) were tested on specimens of the ennessee pigtoe, *Fusconaia barnesiana* (Lea 1838), a species in size (50-80 mm long) and shape that is similar to federally listed congenerics (Fig. 1). Transmitters weighed either 3.5 or 5.5 g (in air), including the

FIG. 1. Radio transmitter with internal coil antenna attached to a specimen of the Tennessee pigtoe.

[1] Reference to trade names or manufacturers does not imply Government endorsement of commercial products.

mercury battery that reportedly provided a tag life of 30 days. Both whip and coiled antennas were tested for range and suitability.

Radio transmitters were attached and covered with commercial epoxy (Tru Bond, Devcon Corp., Chicago, Illinois) and air-dried for 45 min before the animal was submerged (Fig. 1). Tagged specimens were transported to the New River and placed in the substratum at various locations. We used a 10-channel receiver (ATS) with loop antenna (48 mHz range) to locate specimens at least twice weekly for the life of the tags, using the standard triangulation method (Tyus, 1982). After triangulation, we detached the loop antenna and used the receiver directly to pinpoint the location of the tag. Ranges of transmitters with whip and coiled antennas were determined by walking upstream from a transmitter until the signal became inaudible.

We later placed tagged mussels in an artificial circular stream with substratum and observed the movement and orientation of tagged and untagged *Fusconaia barnesiana*, to compare behavior.

Results and Discussion. As judged by field trials with the magnetometer, we concluded that the use of magnets and a portable magnetometer for relocating tagged freshwater mussels is a time- and labor-intensive project, due primarily to the relatively small magnetic field around each magnet and the occurrence of background electromagnetic fields. Naturally occurring magnetized materials such as iron ferrite or magnetite and many types of igneous rock produce fields that essentially render the magnetometer ineffective at its higher scales of sensitivity. Because of natural and anthropogenic sources of electromagnetism in streams and rivers, the detection of small magnets is ineffective except at close range. Magnetometry posed several disadvantages: short range of detection (< 30 cm), background levels of magnetism (noise), restricted water depth of < 0.5 m (length of probe), and the need to use both the instrument meter and audio signal to locate specimens – which is difficult while one is sweeping the probe.

Testing of the various radio transmitters in the river revealed no audible differences in signal strength at water depth < 1.0 m and within 50 m of the transmitter. Ranges of the two types of antennas (0.5 m water depth) were roughly 400 m for the whip antenna and 250 m for the coil antenna, when there were no obstructions between transmitter and receiver. Specimens of *Fusconaia barnesiana* with all tested radio tags were easily relocated by triangulation. Once the intersect location was determined, often within 2-5 m of the radio-tagged mussel, the antenna was removed and the receiver was held above the water surface. At a water depth of roughly 0.6 m at most locations, the transmitter signal was strong enough to locate specimens to within 1 m.

Battery life for the LLE and ATS radio-tags was 3 or 4 weeks. After the batteries died, we returned tagged specimens to the laboratory for observations of behavior in a circular stream with low water velocity (< 20 cm/s). The attached transmitters did not inhibit burrowing of mussels into the substratum, where they remained for about 2 weeks before we released them. However, field observations in the New River indicated that the whip antenna occasionally collected detritus, which probably disturbed the burrowed mussel. Although the length of the whip antenna could be reduced, the range of transmission would also be reduced.

Table 1. Transmitters tested on freshwater mussels in the New River, Virginia.

Source	Weight in air (g)	Antenna type	Dimensions (mm) L W D	Frequency (mHz)
LLE*	3.5	Whip	20 x 12 x 7	48-123
LLE	3.5	Whip	30 x 14 x 6	48-165
LLE	3.5	Coil	30 x 10 x 8	48-142
ATS*	5.5	Coil	20 x 13 x 6	48-190
ATS	3.5	Coil	17 x 9 x 5	48-140

* LLE - L.L. Electronics: ATS - Advanced Telemetry Systems

We concluded that the smaller coil antenna radio tags provide an effective means of relocating mussels to within 1 m. Two key issues on the practicality of radiotelemetry for freshwater mussels are battery life of the transmitter and size of the tags, particularly for use on small endangered species. The tag must be small enough to produce little or no drag and not alter the stability of the mussel when it is burrowed. Commercially produced tags are available for small species, but battery size ultimately determines overall tag size and weight. Batteries (mercury and lithium) now used with small transmitters have relatively short lives because current drains are continuous (Tyus, 1982); consequently, only short-term monitoring of translocated mussels is possible. Transponders are available for radio tags, but they add significantly to tag size. Development of a microchip-controlled tag that would turn itself on and off (e.g., 1 hr each day), at a time selected by the user, would greatly extend battery life and overcome the major liability of the tags available for mollusk telemetry.

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RICHARD J. NEVES, FRED SERVELLO[1], and REBECCA WAJDA[2], *Virginia Cooperative Fish and Wildlife Research Unit*[3] *U.S. Fish and Wildlife Service, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 24061, U.S.A.*

[1]Current address: Department of Forestry and Wildlife, University of Maine, Orono, Maine 04469, U.S.A.

[2]Current address: Virginia Department of Game and Inland Fisheries, P.O. Box 11104, 4010 West Broad Street, Richmond, Virginia 23230, U.S.A.

[3]The Unit is jointly supported by the U.S. Fish and Wildlife Service, Virginia Department of Game and Inland Fisheries, and Virginia Polytechnic Institute and State University.

Malacological Review, 1989, 22: 64-66

DISTRIBUTIONS OF *SPHAERIUM SIMILE* AND *PISIDIUM DUBIUM* (BIVALVIA: SPHAERIIDAE). -- Herrington (1962) gave the distribution of *Sphaerium sulcatum* (Lamarck) [= *Sphaerium simile* (Say)] as "Quebec, Ontario (north to James Bay), Manitoba, Saskatchewan, Alberta, Maine, Massachusetts, New York, New Jersey, Pennsylvania, Virginia, Ohio, Michigan, Indiana, Illinois, Minnesota, South Dakota, Iowa, Montana, Wyoming and Washington?; all north of the Maximum Pleistocene glaciation limit". For *Pisidium dubium* (Say), Herrington (1962) gave the following distribution: "Ontario (Lake Ontario and St. Lawrence River drainage, and Ottawa River near Ottawa), Vermont, Massachusetts, New York, New Jersey, Pennsylvania, District of Columbia, Virginia, South Carolina, Tennessee, Alabama, Georgia, Florida and Michigan" (also see Burch, 1975). Previously, *S. simile* was considered rare in the south and *P. dubium* was purported to range north into the Yukon and Alaska (Dall, 1910; Sterki, 1916). The latter records apparently were for *P. idahoensis* Roper rather than *P. dubium*. Clarke (1981) limited northern distributions of *S. simile* to southern Canada and *P. dubium* only to southern Ontario.

Historical records which were not included in Herrington (1962) or Burch (1975) exist for *Sphaerium simile* and *Pisidium dubium* from the southern United States. East of the Mississippi River, Heard (1963) presented collection localities for both species from as far south as Florida. Sampson (1893, 1894) reported the species as *S. sulcatum* and *P. virginicum* Bourguignat, respectively, from the southern Ozark Plateaus (White River at Eureka Springs, Carroll County, Arkansas). Hinkley (1915) collected several sphaeriids from the White River at Cotter, Baxter County, Arkansas, including *P. dubium, S. striatinum* (Lamarck), and an unidentified *Sphaerium*. Herrington (1962) and Heard (1963) evidently were not able to locate voucher specimens for the Ozark records. Based on the authority of previous reports, Gordon (1981) subsequently listed *P. dubium* in the molluscan fauna of Arkansas but overlooked *S. simile*. Mackie & Huggins (1983) since have found a fairly wide distribution of *S. simile* in Kansas; however, the species has not been reported from adjacent states to the west or south (see Wu, 1978; Branson, 1981).

Several populations of *Sphaerium simile* and *Pisidium dubium* have been rediscovered within the Ozark portion of the White River basin (Fig. 1; representative vouchers are deposited in the University of Colorado Museum, Nos. 32749 and 32750). These records corroborate the earlier species accounts of Sampson (1893, 1894) and Hinkley (1915) and establish the distribution of *P. dubium* west of the Mississippi River. Since only two species of *Sphaerium* presently are recognized from the region (*S. striatum, fide* Gordon, 1981, and *S. simile*, herein), Hinkley's (1915) generic-level use of *Musculium* (sometimes considered a subgenus of *Sphaerium*: *e.g.*, Clarke, 1981) suggests that his unidentified *Sphaerium* may have been *S. simile*. In conjunction with Mackie & Huggins (1983), the distribution of *S. simile* west of the Mississippi River is extended considerably south of the Pleistocene glaciation, comparable to its range in the southeastern United States (see Heard, 1963). A similar geographic pattern has been demonstrated for *P. fallax* Sterki (Gordon, Mackie, & Brown, 1980).

As with *Pisidium fallax, Sphaerium simile* has been considered a northern species. Pleistocene glaciation forced such species to shift ranges to the south. Geologic provinces (*e.g.*, Interior Highlands, Cumberland region) functioned as faunal refugia during these periods and dispersal centers following glacial retreat. Relict populations have persisted in these regions by inhabiting cool-water habitats (*e.g.*, spring runs). The Pleistocene refugial hypothesis previously has been applied to the distributions of some Unionoidea in the Interior Highlands (Gordon, Kraemer, & Brown, 1980; Johnson, 1980).

All three of the recent Ozark localities represented cool-water habitats: one from considerable spring-run influxes (upper North Fork of the White River); the other two from discharges of hypolimnetic release dams (Bull Shoals and Norfork reservoirs). In the

FIG. 1. Localities of *Sphaerium simile* and *Pisidium dubium* in the Ozark Plateaus. ● = recent sites; O = historical site.

upper North Fork, substrates ranged from silt to cobble and a moderated temperature annually fluctuated between 9-28°C (Gordon, 1987). Specimens were located in most microhabitats sampled, but both species tended to be aggregated in slow-water areas possessing substrates of silt to fine sand mixed with detritus (primarily sites 1 and 2 *in* Gordon, 1987). At the other two localities, populations also preferred fine particle/detritus substrates but were found only in backwater areas. Annual temperature ranges were comparable to pre-impoundment values (0-26°C, White River at Cotter, Baxter County, Arkansas: Saunders & Billingsley, 1950; U.S. Geological Survey, 1978); however, hypolimnetic discharges could cause diel fluctuations as great as 15°C (*e.g.*, 8.5-23.5°C, 27 June, 1977, White River at Cotter: U.S. Geological Survey, 1978). On a microhabitat level, numerous spring-run influxes in the area and the insulatory quality of backwater situations may moderate somewhat the effects of these acute thermal fluctuations.

Generally, observed environmental conditions were similar to previously reported habitats (see Burch, 1975). Teal (1957) identified *Pisidium dubium* as a component of cold spring communities (Concord, Massachusetts: 8-11.5°C, annually) and Clarke (1981) found *Sphaerium simile* to range throughout much of the Canadian boreal forest zone. Waite & Neufeld (1977) observed that respiration rates of *S. simile* exhibited relative thermal insensitivity within a range of 15-25°C. These data suggest that *S. simile* may be adapted physiologically to thermally moderated environments. Tolerance to or preference for cool-water habitats is indicated, thus lending credence to the Pleistocene refugial hypothesis for the Ozark populations.

Acknowledgement. Identifications were confirmed by Dr. Gerry L. Mackie, University of Guelph.

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MARK E. GORDON, *Tennessee Cooperative Fishery Research Unit, Department of Biology, P.O. Box 5114, Tennessee Technological University, Cookeville, Tennessee 38505, U.S.A.*

PUBLICATIONS

The list of publications below is divided into the following headings, presented alphabetically: Behavior; Bibliographies and Biographies; Control; Culture; Cytology, Histology and Morphology; Ecology and Natural History; General; Genetics; Geographical Distribution and Faunal Lists; Methods; Paleontology and Evolution; Physiology and Biochemistry; Reproduction and Development; Snail Hosts, Parasites and Parasitism; and Systematics and Nomenclature. Publications listed here do not include articles published in malacological serial publications (see pp. 95-172).

Anthropology & Archaeology

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Archiv für Molluskenkunde

der Senckenbergischen Naturforschenden Gesellschaft
Organ der Deutschen Malakozoologichen Gesellschaft

Begrürdet von Prof. Dr. W. Kobelt
Weitergeführt von Dr. W. Wenz, Dr. F. Haas und Dr. A. Zilch
Herausgegeben von Dr. R. Janssen

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ISRAEL JOURNAL OF MALACOLOGY

PUBLISHED BY THE ISRAEL MALACOLOGICAL SOCIETY
AND THE MUNICIPAL MALACOLOGICAL MUSEUM, NAHARIYA

Correspondence address: I.M.S. c/o H.K. Mienis, Kibbutz Netzer Sereni, 70-395, Israel

Volume 7, No. 5 31 Oct. 1981

SPECIES COMPOSITION, GEOGRAPHICAL DISTRIBUTION AND HABITAT CHARACTERISTICS OF ROCKY INTERTIDAL CERITHIIDAE (GASTROPODA; PROSOBRANCHIA) ALONG THE RED SEA SHORES OF SINAI[1]

Yoram Ayal[2] and Uriel N.Safriel
Department of Zoology, The Hebrew University of Jerusalem

Basteria ISSN·0005·6219

TIJDSCHRIFT VAN
DE NEDERLANDSE MALACOLOGISCHE VERENIGING

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REDACTIE: Dr. A.C. van Bruggen en Dr. E. Gittenberger.
Redactie-adres: Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Postbus 9517, 2300 RA Leiden.
De redactie wordt bijgestaan door een redactieraad van prominente malacologen.

Basteria

ISSN-0005-6219

TIJDSCHRIFT VAN
DE NEDERLANDSE MALACOLOGISCHE VERENIGING

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Bollettino Malacologico

PUBBLICAZIONE MENSILE EDITA DALLA
SOCIETÀ ITALIANA DI MALACOLOGIA
c/o Acquario Civico, Viale Gadio 2 - 20121 Milano

Anno XXIII - N. 11-12 novembre-dicembre 1987

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Titolo precedente: «CONCHIGLIE» fino al 1978 (Anno XIV - n. 11-12).

DIRETTORE SCIENTIFICO: Giulio Melone

REDAZIONE: Giorgio Barletta, Fernando Ghisotti

SOCIETÀ ITALIANA DI MALACOLOGIA

SEDE SOCIALE: **c/o Acquario Civico, Viale Gadio 2, 20121 Milano**

Direttore Responsabile: Fernando Ghisotti

AUTORIZZAZIONE TRIBUNALE DI MILANO N. 479 DEL 15 OTTOBRE 1983
SPEDIZIONE IN ABBONAMENTO POSTALE - GRUPPO IV/70

Bollettino Malacologico

PUBBLICAZIONE MENSILE EDITA DALLA
SOCIETÀ ITALIANA DI MALACOLOGIA
c/o Acquario Civico, Viale Gadio 2 - 20121 Milano

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Viale Gadio, 2 - 20121 Milano (MI)

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SOCIETÀ ITALIANA DI MALACOLOGIA
c/o Acquario Civico, Viale Gadio 2 - 20121 Milano

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ISSN 0394-7149

Direttore Responsabile: Fernando Ghisotti

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BULLETIN OF THE INSTITUTE OF MALACOLOGY TOKYO

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6-36, MIDORICHO 3 CHOME,
TANASHI CITY, TOKYO 188, JAPAN

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(Publicado en agosto de 1988)

Correspondence must be addressed to:

Secretario de la
Sociedad Malacológica del Uruguay

Jorge Pita
Casilla de Correo Nº 1401
MONTEVIDEO URUGUAY

FOLIA
MALACOLOGICA

BULLETIN 1

CRACOW — 1987

BULLETIN 1

ANDRZEJ FALNIOWSKI

HYDROBIOIDEA OF POLAND (PROSOBRANCHIA: GASTROPODA)

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SOCIETE FRANCAISE DE MALACOLOGIE

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Direction de la publication : J. DAGUZAN - Président de la S.F.M.
Gérants du volume : Claude POIZAT et Nardo VICENTE.

Imprimé à MARSEILLE - Faculté des Sciences
et Techniques St-Jérôme - 13013 MARSEILLE

Dépôt légal : 4ème trimestre 1988

Heldia

MÜNCHNER MALAKOLOGISCHE MITTEILUNGEN

HERAUSGEBER:

HANS D. BOETERS GERHARD FALKNER JÜRGEN WERNER

SEKRETARIAT: MARGRIT FALKNER

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Postfach 26 01 23, 8000 München 26, BRD

Redaktionsanschrift: Raiffeisenstraße 5, 8059 Wörth-Hörlkofen, BRD • Tel.: 0 81 22/71 32

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MÜNCHNER MALAKOLOGISCHE MITTEILUNGEN

HERAUSGEBER:

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SEKRETARIAT: MARGRIT FALKNER

Heldia	Band 1	Sonderheft 1	S. 1-38, Tafeln 1-5	München, Mai 1987

Land- und Süßwassermollusken der Maltesischen Inseln.

Von

KARL-HEINZ BECKMANN,

Ascheberg-Herbern.

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Einzelverkaufspreis dieses Sonderhefts DM 35,– (zuzüglich Porto und Verpackung).

Die verbesserte Ausstattung dieses Heftes wurde dankenswerterweise durch einen namhaften Druckkostenbeitrag des Autors ermöglicht.

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ISSN 0212-3010

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Levantina No. 26-27 ISSN 0334-3715 May-July 1980

We deeply mourn the sudden loss of our dear friend
KURT GEISEL
and extend our condolences to the bereaved family

the Board of the
Israel Malacological Society

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Kurt Alexander Geisel
(25 May 1918 - 10 July 1980)
as a tribute for all the work he has done for
the Israel Malacological Society

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LEVANTINA

ISSN 0334 - 3715

A JOURNAL OF MALACOLOGY

PUBLISHED BY THE ISRAEL MALACOLOGICAL SOCIETY

Correspondence address: I.M.S. c/o H.K. Mienis, Kibbutz Netzer Sereni, 70-395, Israel

nos. 54-59 1985

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LEVANTINA

ISSN 0334 - 3715

A JOURNAL OF MALACOLOGY

PUBLISHED BY THE ISRAEL MALACOLOGICAL SOCIETY

Correspondence address: I.M.S. c/o H.K. Mienis, Kibbutz Netzer Sereni, 70-395, Israel

nos. 60 – 65 1986

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PUBLISHED BY THE ISRAEL MALACOLOGICAL SOCIETY

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Price: US$ 48.00 (postpaid)

Malacological Review
P. O. Box 3037
Ann Arbor, MI 48106, U.S.A.

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EDITOR-IN-CHIEF
Dr. M. G. Harasewych
Division of Mollusks
National Museum of
Natural History
Smithsonian Institution
Washington, DC 20560

NORTH PACIFIC SHELLS

Occasional Publication of

The Institute of Malacology, Tokyo
6-36, Midoricho 3 chome
Tanashi City, Tokyo 188, Japan

Authors: Ranji Tiba and Sadao Kosuge

1. Genus *Volutopsius* Moerch	November, 1979
2. Genus *Arctomelon* Dall	June, 1980
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Bács-kiskun Megyei Szervezete
Felelős kiadó: Konfár Sándor

16 1988

SOOSIANA

A TUDOMÁNYOS ISMERETTERJESZTŐ TÁRSULAT
BÁCS-KISKUN MEGYEI SZERVEZETE
BIOLÓGIAI SZAKOSZTÁLYÁNAK
IDŐSZAKOS MALAKOLÓGIAI KÖZLEMÉNYEI

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贝类学论文集

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No. 2

1986

中国贝类学会 编辑

Edited by the Chinese Society of Malacology

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中国贝类学会 编辑

科学出版社

THE
VELIGER

A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

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VELIGER

A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
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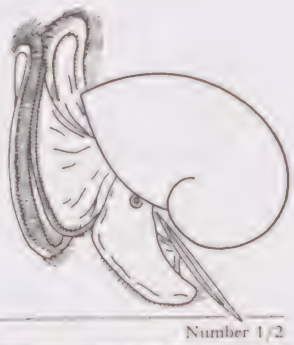
R. Stohler, Founding Editor



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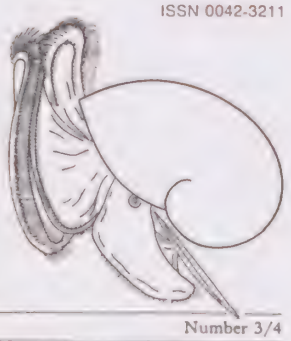
ISSN 0042-3211

THE VELIGER



A Quarterly published by
CALIFORNIA MALACOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

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The Veliger (ISSN 0042-3211) is published quarterly on the first day of July, October, January and April. Rates for Volume 31 are $28.00 for affiliate members (*including* domestic mailing charges) and $56.00 for libraries and nonmembers (*including* domestic mailing charges). An additional $4.00 is required for all subscriptions sent to foreign addresses, including Canada and Mexico. Further membership and subscription information appears on the inside cover. The Veliger is published by the California Malacozoological Society, Inc., % Department of Zoology, University of California, Berkeley, CA 94720. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to C.M.S., Inc., P.O. Box 9977, Berkeley, CA 94709.

VENUS

THE JAPANESE JOURNAL OF MALACOLOGY

第46巻 第3号 東京 Tokyo **Vol. 46 No. 3**

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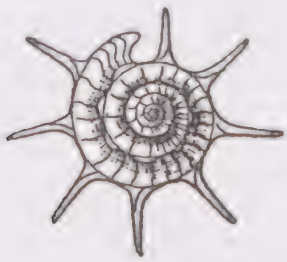

日本貝類学会

Published by

THE MALACOLOGICAL SOCIETY OF JAPAN

昭和62年10月 October 1987

東京 Tokyo

貝 雑
VENUS
(Jap. Jour. Malac.)

ISSN : 0042—3580

貝類学雑誌

VENUS

THE JAPANESE JOURNAL OF MALACOLOGY

第46巻 第4号 Vol. 46 No. 4

昭和62年12月 December 1987

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THE WESTERN SOCIETY OF MALACOLOGISTS

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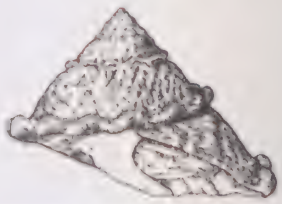

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AARTSEN, J.J. van, Adm. Helfrichlaan 33, 6952 GB Dieren, The Netherlands [102, 103, 105, 106]
ABBE, George R., Academy of Natural Sciences, Benedict Estuarine Research Laboratory, Benedict, Maryland 20612, U.S.A. [124]
ABSALÃO, Ricardo Silva, Department de Zoologia, Instituto de Biologia, C.C.S., Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro, 21940, Brasil [155]
ACOSTA, C., Centro Experimental de Vilaxoán, Consellería de Pesca, Xunta de Galicia, Apdo. 208. Villagarcía de Arosa, Spain [116]
ADAMS, William F., Environmental Resources Branch, U.S. Army Corps of Engineers, P.O. Box 1890, Wilmington, NC 28402, U.S.A. [155]
AGUILAR ROSAS, Luis E., Instituto de Investigaciones Oceanologicas, Universidad Autonoma de Baja California, Apartado Postal 453, Ensenada, Baja California, Mexico [169]
AIREY, William J., 59 Valley Park Drive, Clanfield, Hants, PO8 0PL, U.K. [119]
ALDANA ARANDA, Dalila, CINVESTAV IPN Mérida, A.P. 73 Cordemex, C.P. 97610, Mérida, Mexico [112]
ALEXANDROWICZ, Stefan Witold, S. Staszic Academy of Mining and Metallurgy, Institute of Geology and Mineral Deposits, Al. Mickiewicza 30, 30-059 Kraków, Poland [110]
ALLEN, Standish K., University of Maryland, Baltimore, Maryland 21202, U.S.A. [171]
ALONSO, Maria Rosario, Departamento de Zoología, Facultad de Biología, Universidad de La Laguna, Tenerife, Islas Canarias, Spain [100]
AMANO, Kazutaka, Department of Geoscience, Joetsu University of Education, Yamayashiki-cho, Joetsu City, Niigata Pref., 943, Japan [169]
AMBROSE, Richard F., Marine Science Institute, University of California, Santa Barbara, California 93106, U.S.A. [148]
AMELA SIURANA, J.F., Dpto. Zoología, Fac. C. Biológicas, Univ. Valencia; Dr. Moliner, 50 Burjasot 46100 Valencia, Spain [116]
ANADON, R., Dpto. de Biologia de Organismos y Sistemas, Universidad de Oviedo, 33005 Oviedo, Spain [119]
ANCELET, Robert, Louisiana Department of Wildlife and Fisheries, 400 Royal, New Orleans, Louisiana 70130, U.S.A. [123]
ANDERSON, Roland C., Seattle Aquarium, Pier 59, Seattle, Washington 98101, U.S.A. [171, 172]
ANDO, Yasuji, 4-15-9, Taiji, Akashi 673, Japan [168]
ANDRIGUETTO, José Milton, Jr., Zoology Department, Universidade Federal Do Paraná, Cx.P. 3034, CEP 80.001, Curitiba, Pr., Brazil [96]
ANGULO, Eduardo, Laboratorio de Zoología, Dpto. de Biología, Facultad de Ciencias, Universidad del País Vasco, Aptdo. 644, 48080 Bilbao, Spain [115]
ANT, Herbert, Westfälische Wilhelmsuniverität, Lehrgebiet Biologie, Abteilung Ökologie, Fliednerstraße 21, 4400 Münster/Westf., F.R. Germany [114]
ANTONOVITS, Dániel, Budaörs, Szivárvány u. 8., H-2040, Hungary [158]
APARICIO, M.T., Museo Nacional de Ciencias Naturales, (C.S.I.C.), Jose Gutierrez Abascal 2, 28006 Madrid, Spain [121]
ARTER, Hubert E., Department of Zoology, University of California, Berkeley, California 94720, U.S.A. [172]
ARY, Roy D., Jr., Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70148, U.S.A. [1222, 123]
ASAKURA, Akira, Amakusa Marine Biological Laboratory, Kyushu University, Tomioka, Reihoku, Amakusa-gun, Kumamoto-ken, 863-25, Japan [168]
ASKEW, Timothy M., Harbor Branch Oceanographic Institution, Inc., 5600 Old Dixie Highway, Fort Pierce, FL 34946, U.S.A. [155]
AUBERT, C., Institut Technique de l'Aviculture et des petits élevages (ITAVI), 31 Rue du Maréchal Joffre, B.P. 647, 35008 Rennes Cedex, France [120]
AUFFENBERG, Kurt, Malacology Division, Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A. [156]
AUGUSTYN, C.J., Sea Fisheries Research Institute, Private Bag X2, Rogge Bay 8012, Cape Town, Republic of South Africa [148]
AVNIMELECH, M., [no address given] [133]
AYAL, Yoram, Nature Reserves Authority, 78 Yirmeyahu St., Jerusalem 94467, Israel [101]
AZUMA, Masao, 13-7, Hobai-1, Takarazuka City, 665, Japan [167, 168]
AZUMA, Yoshio, 13-7, Hobai-1, Takarazuka City, 665, Japan [167]

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BABA, Károly, Szeged, Vár utca 6, H-6720, Hungary [158, 159, 160]
BABA, Kikutarô, Shigigaoka 35, Minami-11-jyo, Sango-cho, Ikoma-gun, Nara-ken, 636, Japan [167, 169]
BAETEN, Stéphane, Institut National Agronomique, 43 av. Ch. Nicolle, Tunis, 1002, Tunisia [111]
BAGLIVO, Jenny A., Department of Mathematics and Computer Science, Fairfield University, Fairfield, Connecticut 06430, U.S.A. [123]
BAHAMONDES-ROJAS, Ingrid, Laboratoire de Biologie et Biochimie Marines, Université de Poitiers I.U.T. rue de Roux 17026, La Rochelle, France [111]
BALCH, Norval, Aquatron Laboratory, Dalhousie University, Halifax, Nova Scotia, B3H 4J1 Canada [148]
BANDEL, Klaus, Universität Hamburg, Geologisch-Paläontologisches Institut und Museum, Bundesstrasse 55, 2000 Hamburg 13, F.R. Germany [151]
BANK, R.A., Crijnssenstraat 61 hs, NL 1058 XV, Amsterdam, The Netherlands [102, 103, 113]
BAO, Zhengying, Guangxi Institute of Parasitic Diseases Control, China [162]
BAQUEIRO, Erik, Apartado postal 587, Campeche, Camp., Mexico [126]
BAR, Ze'ev, M.L. Kinglaan 356, 1111 LR Diemen, Holland [129, 130, 132, 133, 137]
BARASH, Al, Via delle Viole 7, 57100 Livorno, Italy [104, 132, 133, 136, 144]
BARBER, Bruce J., Department of Oyster Culture, New Jersey Agricultural Experiment Station, Cook College, Rutgers University, Shellfish Research Laboratory, P.O. Box 687, Port Norris, New Jersey 08349, U.S.A. [124]
BARCELLOS, L.J., Investigador del Museo Oceanográfico de la FURG, Fundação Universidade de Rio Grande, RS, Uruguay [109]
BARKAI, R., Zoology Department and Marine Biology Research Institute, University of Capetown, Rondebosch 7700, South Africa [119]
BARNHART, M. Christopher, 4662 Mt. La Plata Drive, San Diego, California 92117, U.S.A. [171]
BARRAJON, Agustín, C/Nuzas, Bl. 7-5°-A, 29010-Málaga, Spain [164]
BARTELL, Clelmer K., Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70148, U.S.A. [122, 123]
BARTER, Janeen, State of Maine Department of Marine Resources, West Boothbay Harbor, Maine 04575, U.S.A. [124]
BAUDET, Joseph, Laboratoire de Biologie marine, Faculté des Sciences et Techniques 2, rue de la Houssinière, 44 072 Nantes Cedex 03, France [111]
BAUR, Anette and Bruno, Department of Zoology, Uppsala University, Box 561, S-751 22 Uppsala, Sweden [164]
BEATTIE, J. Harold, College of Fisheries, University of Washington, Seattle, Washington 98195, U.S.A. [123]
BEAUGEZ, Kathy, Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39564, U.S.A. [126]
BECH, Miquel, C/. Córcega, 404, 08027 Barcelona, Spain [117]
BECK. M., [no address given] [134]
BECKMANN, Karl-Heinz, Schüttwall 34, 4715 Ascheberg-Herbern, F.R. Germany [115]
BEGOSSI, A., Departamento de Zoologia, IB, UNICAMP, C.P. 6109, Campinas, 13081, SP, Brazil [150]
BEHRENS, David W., Pacific Gas and Electric Company, Biological Research Laboratory, P.O. Box 117, Avila Beach, California 93424, U.S.A. [166]
BENYAHIA, M., Laboratoire d'Ecologie, 1 Rue des Récollets, 57000 Metz, France [112]
BERGSTROM, Peter W., Department of Biology, Washington & Lee University, Lexington, Virginia 24450, U.S.A. [149]
BERNARD, F.R., Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada [172]
BERNASCONI, Reno, Hofwilstraße 9, CH-3053 Münchenbuchsee, Switzerland [113, 114]
BERRIGAN, Mark E., Florida Department of Natural Resources, Division of Marine Resources, Tallahassee, Florida 32399, U.S.A. [125]
BERTSCH, Hans, Research Associate, Malacology, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. [131, 164, 165, 171, 172]
BIEDERMANN, W., Universität - Gesamthochschule - Duisburg, Fachbereich 6, Zoologie, Lotharstraße 65, D - 4100 Duisburg 1 (BRD), F.R. Germany [154]
BIELER, Rüdiger, Smithsonian Marine Station at Link Port, 5612 Old Dixie Highway, Fort Pierce, Florida 34946, U.S.A. [151, 164]
BISKER, Robert, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Eastern Shore Laboratory, Wachapreague, Virginia 23480, U.S.A. [122, 123]
BLEAKNEY, J. Sherman, Biology Department, Acadia University, Wolfville, Nova Scotia, B0P 1X0, Canada [166]
BLOCHER, Manfred, Duisberg, F.R. Germany [141]

BLOGOSLAWSKI, Walter, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460, U.S.A. [126]
BOETERS, Hans D., Karneidstraße 8, D-8000 München 90, F.R. Germany [100, 103, 113, 114, 115]
BOGI, Cesare, Via delle Viole 7, 57100 Livorno, Italy [104, 105]
BOGNAR, Ferenc, Budapest, Szentmihályi ut 20-22.III.84, H-1144, Hungary [158]
BOISMERY, Jean, Laboratoire de Zoologie, Université de Caen, 14032 Caen Cedex, France [111]
BONNIN, Juan, Dpto. Zoología, Facultad de Ciencias Biológicas, Univ. Valencia; Dr. Moliner, 50 Burjasot 46100 (Valencia), Spain [116]
BORJA, Angel, Servicio de Investigación Oceanográfica del Gobierno Vasco, Departamento de Agricultura y Pesca, Avda. Satrustegui 8, 20008 San Sebastián, Spain [116, 117]
BOSS, Kenneth J., Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, U.S.A. [155, 166]
BOTTON, Mark L., Division of Science and Mathematics, Fordham University, College at Lincoln Center, New York, New York 10023, U.S.A. [126]
BOUCHER-RODONI, Renata, Laboratoire Arago, 66650 Banyuls-sur-Mer, France [148]
BOUCHET, Philippe, Muséum National d'Histoire Naturelle, 55, rue de Buffon, 75005 Paris Cedex 05, France [106, 156, 169]
BOURNE, N., Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada [126]
BOURNE, N.B., Dept. of Zoology, University College Cardiff, Cardiff CF1 1XL, Wales, U.K. [121]
BOUTILLIER, J.A., Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada [122, 126]
BOWEN, I.D., Dept. of Zoology, University College Cardiff, Cardiff CF1 1XL, Wales, U.K. [121]
BOYLE, P.R., Department of Zoology, University of Aberdeen, Scotland [148]
BRADNER, Hugh, Scripps Institution of Oceanography, La Jolla, California 92093, U.S.A. [171]
BRATCHER, Twila, Los Angeles County Museum of Natural History, Malacology Section, Exposition Park, Los Angeles, California 90007, U.S.A. [164]
BRETON, Yvan, Dept. Anthropologie, Université Laval, Québec, Canada [125]
BRIARD, Pascal, Station de Zoologie, INRA, 28 rue de Herrlisheim, B.P. 507, 68021 Colmar cédex, France [111]
BRODIE, G., Institute of Natural Resources, University of the South Pacific, Suva, Fiji [121]
BROUSSEAU, Diane J., Department of Biology, Fairfield University, Fairfield, Connecticut 06430, U.S.A. [123]
BROWN, Carolyn, U.S. Department of Commerce, NOAA, National Marine Fisheries Service, 1335 East-West Highway, Silver Spring, Maryland 20910, U.S.A. [126]
BULLOCK, Robert C., Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A. [126, 166]
BURCH, J.B., Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A. [128, 170]
BURGESS, C.M. (Pat), [no address given] [133]
BURNAY, Luis P., Centro de Zoologia, Rua da Junqueira 14, 1300 Lisboa, Portugal [151]
BURRESON, Eugene M., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [124]
BURSTEIN, Avi, 1, Harel Street, 34555 Haifa, Israel [138]
CABARET, J., INRA, Station de Pathologie Aviaire et de Parasitologia, Unité d'Ecologie Parasitaire, 37380 Monnaie, France [120]
CAI, Yingya, Zhangjiang Fisheries College, China [162]
CALOW, P. Department of Animal Biology, University of Sheffield, Sheffield S10 2TN, England, U.K. [120, 121]
CAMPOS-GONZALEZ, Ernesto, Escuela Superior de Ciencias, Universidad Autónoma de Baja California, Apartado Postal 2300, Ensenada, B.C., México [164]
CANZONIER, W.J., Rutgers University, Department of Oyster Culture, Port Norris, New Jersey 08349, U.S.A. [125]
CAPROTTI, Erminio, Via Ollearo 3, 20155 Milano, Italy [104, 105]
CAREFOOT, Thomas H., Department of Zoology, University of British Columbia, Vancouver, V6T 2A9, Canada [164, 165]
CARLTON, James T., Oregon Institute of Marine Biology, Department of Biology, University of Oregon, Charleston, Oregon 97420, U.S.A. [165]
CARPENA, Francisco, C/Nuzas, Bl. 7-6°-A, 29010-Málaga, Spain [164]
CARRIKER, Melbourne R., College of Marine Studies, University of Delaware, Lewes, Deleware, 19958, U.S.A. [124]
CARRU, Anne-Marie, Laboratoire de Chimie Analytique, Institut d'Hydrobiologie et de Climatologie, Tour 26, 4éme étage, 4 Place Jussieu, 75005 Paris, France [149]

CASTAGNA, Michael, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Eastern Shore Laboratory, Wachapreague, Virginia 23480, U.S.A. [122, 123, 126]
CASTILLA, Juan C., Estación Costera de Investigaciones Marinas, Las Cruces, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile [123]
CASTILLEJO, José, Departamento de Biología Animal, Facultad de Biología, Universidad de Santiago de Compostela, Spain [117]
CASTILLO, Daniel, Escuela Superior Politecnica de Litoral, Facultad de Ingeniera Maritima y Ciencias del Mar, Guayaquil, Ecuador [126]
CASTRO, Kathleen M., Department of Fisheries, Aquaculture and Veterinary Science and the International Center for Marine Resource Development, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A. [126]
CATALANO, E., Institute of Zoology, University of Palermo, Via Archirafi 18 -- 90123 Palermo, Italy [149]
CATTANEO-VIETTI, R., Instituto di Zoologia dell'Università di Genova, Italy [102]
CECALUPO, Alberto, Via Zurigo 28/4, 20147 Milano, Italy [105]
CERVERA, J.L., Departamento de Zoología, Facultad de Biología, Univ. Sevilla, Ap. 1095, Reina Mercedes s/n. 41012 Sevilla, Spain [149]
CHALERMWAT, Kashane, Nelson Biological Labs, Rutgers University, Piscataway, New Jersey 08856, U.S.A. [166]
CHANG, Kuan Min, Department of Oral Surgery, College of Medicine, National Taiwan University, Taipei, Taiwan, Republic of China [108]
CHAO, David, Department of Parasitology, National Yang-Ming Medical College, Republic of China [108]
CHAPMAN, Samuel R., Ira C. Darling Center, University of Maine, Walpole, Maine 04573, U.S.A. [124]
CHARRIER, Maryvonne, Laboratoire de Zoologie générale et d'Ecophysiologie (L.A. INRA), Université de Rennes I, Campus de Beaulieu, Avenue de Général Leclerc, 35042 Rennes Cedex, France [112]
CHATFIELD, June E., The Oates Memorial Library and Museum and The Gilbert White Museum, The Wakes, Selborne, Alton, Hampshire GU34 3JH, England, U.K. [118]
CHATRY, Mark F., Louisiana Department of Wildlife and Fisheries, Lyle S. St.. Amant Marine Laboratory, P.O. Box 37, Grand Isle, Louisiana 70358, U.S.A. [125]
CHELAZZI, G., Dipartimento di Biologia Animale e Genetica, Università degli Studi di Firenze, Via Romana 17, 50125 Florence, Italy [120]
CHEN, Chengchong, Nanhai Fisheries Institute, China [162]
CHEN, Kaiping, Shanghai Fisheries College, China [162]
CHEN, Liuyan, Institute of Parasitic Diseases, Hupei Academy of Medical Sciences, China [162]
CHEN, Pulin, Institute of Parasitic Diseases, China National Centre for Preventive Medicine, China [161]
CHEN, Qiyu, Institute of Hydrobiology, Academia Sinica, China [161]
CHEN, Wenlong, Fujian Fisheries Institute, China [163]
CHENG, Xianqiu, Human Institute of Parasitic Disease Control, China [162]
CHEW, Kenneth, College of Fisheries, University of Washington, Seattle, Washington 98195, U.S.A. [123]
CHO, Dong-Hyon, Department of Biology, Kangweon National University, Korea [128]
CHOE, Rim Soon, Department of Biology, College of Science, Yonsei University, Seoul, Korea [128]
CHRISTIAENS, J., J. Lipsiuslaan, 26, B-3500 Hasselt, Belgium [98]
CHU, Fu-Lin E., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [124]
CHUN, J.H., Department of Preventive Medicine and Institute of Industrial Medicine, Inje College, Pusan, Korea [127]
CHUNG, Pyung-Rim, Department of Parasitology, College of Medicine, Yonsei University, Seoul, Korea [127, 128]
CHUNG, Yong-Jae, Department of Science Education, Ewha Woman's University, Korea [128]
COAN, Eugene V., Research Associate, Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [165, 171, 172]
COLE, M.T., Department of Biological Sciences, Nicholls State University, Thibodaux, Louisiana 70310, U.S.A. [126]
COLGAN, Mitchell W., Earth Science Board, University of California, Santa Cruz, California 95064, U.S.A. [172]
COLLINS, Timothy M., Department of Geology and Geophysics, Yale University, New Haven, CT 06520, U.S.A. [155]

COLMAN, J.G., Department of Earth Sciences, University College, Singleton Park, Swansea, SA2 8PP, U.K. [120]
CONEY, C. Clifton, Los Angeles County Museum of Natural History, Los Angeles, California 90007, U.S.A. [171]
CONNELL, Joseph H., Department of Biological Sciences, University of California, Santa Barbara, California 93106, U.S.A. [166]
CORDERO-DEL-CAMPILLO, M., Laboratorio de Parasitología, Facultad de Veterinaria, León, Spain [119]
CORNI, M. Grazia, Instituto di Zoologia, dell'Università di Bologna, Italy [122]
COSTIL, Katherine, Laboratoire de Zoologie générale et d'Ecophysiologie (L.A. INRA), Université de Rennes I, Campus de Beaulieu, Avenue de Général Leclerc, 35042 Rennes Cedex, France [112]
COX, Carrollyn, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [126, 166]
CRITCHFIELD, Richard, [no address given] [133]
CROCHARD, C., Laboratoire d'Ecologie, 1 Rue des Récollets, 57000 Metz, France [111, 112]
DAGUZAN, Jacques, Laboratoire de Zoologie générale et d'Ecophysiologie (L.A. INRA), Université de Rennes I, Campus de Beaulieu, Avenue de Général Leclerc, 35042 Rennes Cedex, France [112]
DA MOTTA, A.J., 1118-1120 Mody Road, Tsimshatsui East, Kowloon, Hong Kong [114]
DAN, Victor, P.O. Box 1120, Manila, Philippines [107]
DANIN, Z., Department of Zoology, Tel-Aviv University, Israel [132, 133, 136]
D'ASARO, Charles N., Department of Biology, University of West Florida, Pensacola, Florida 32514, U.S.A. [156]
D'ATTILIO, Anthony, Department of Marine Invertebrates, San Diego Natural History Museum, San Diego, CA 92101, U.S.A. [107, 155]
DAVENPORT, John, Animal Biology Group, Marine Science Laboratories, University College of North Wales, Menai Bridge, Gwynedd LL59 5EH, Wales, U.K. [121]
DAVIS, Jonathan P., School of Fisheries, WH-10, University of Washington, Seattle, Washington 98195, U.S.A. [126]
DAWE, E.G., Science Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada [148]
DAY, Elizabeth A., Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, New York 11794-5000, U.S.A. [126]
DEALTERIS, Joseph T., Department of Fisheries, Aquaculture and Pathology, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A. [123, 124, 126]
DEFEO, Omar, Sección Recursos Bentónicos, Instituto Nacional de Pesca (INAPE), Casilla de Correo 1612, Montevideo, Uruguay [109]
DELL'ANGELO, Bruno, Via Follereau 10, 41043 Formigine (MO), Italy [106]
DELONGUEVILLE, C., Av. Den Doorn, 5, B-1180 Bruxelles, Belgium [98]
DEN HARTOG, J.C., Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, 2300 RA Leiden, The Netherlands. [102]
DE WILDE, J.J., Institut Royal des Sciences naturelles de Belgique, Section des Invertébrés récents, Rue Vautier, 29, B-1040 Bruxelles, Belgium [98]
DE WINTER, A.J., c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, 2300 RA Leiden, The Netherlands [102]
DIEZ-BAÑOS, P. & N., Laboratorio de Parasitología, Facultad de Veterinaria, León, Spain [119]
DIJKEMA, Regner, Netherlands Institute for Fishery Investigations, Yerseke, The Netherlands [125]
DIJKSTRA, H.H., Gravinneweg 12, 8604 CA Sneek, The Netherlands [103]
DING, Baoliang, Nanjing Institute of Geology and Mineral Resources, China [163]
DIOURIS, Marcel, Laboratoire de Physiologie Végétale, Université de Bretagne Occidentale, 29287 Brest Cédex, France [112, 126]
DISALVO, Louis H., Department of Aquaculture, Universidad del Norte, Casilla 480, Coquimbo, Chile [164]
DOMOKOS, Tamás, Békéscsaba, Munkácsy Mihály Muzeum, Postafiók 46, H-5601, Hungary [158]
DONVAL, Anne, Laboratoire de Zoologie, Faculté des Sciences, 29287 Brest Cedex, France [112]
DRAPER, Bertram C., Museum Associate in Invertebrate Zoology, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. [171]
DREDGE, M.C.L., Queensland Department of Primary Industries, Fisheries Research Station, Burnett Heads 4670, Queensland, Australia [122, 125]
DROZDOWSKI, Arnold, Instytut Biologii, Uniwersytet M. Kopernika w Toruniu, ul. Gagarina 9, 87 - 100 Torun, Poland [151, 152, 153,]
DUARTE, L.F.L., Departamento de Zoologia, IB, UNICAMP, C.P. 6109, Campinas, 13081, SP, Brazil [150]
DUCHAMPS, Ralph, Avenue Mozart, 52, B 1190 Bruxelles, Belgium [97]
DUGAN, Eleanor E., [no address given] [135]

DUGAS, Ronald J., Louisiana Department of Wildlife and Fisheries, 400 Royal St., New Orleans, Louisiana 70130, U.S.A. [126]
DUMOULIN, E., De Wulk 8, B 8390 Knokke-Heist, Belgium [102]
DUSHANE, Helen, 15012 El Soneto Drive, Whittier, California 90605, U.S.A. [166]
DYDUCH-FALNIOWSKA, Anna, Research Center for the Protection of Nature and Natural Resources, ul. Arianska 1, 31-512 Kraków, Poland [110]
EDLINGER, Karl, Institut für Zoologie, Universität Wien, Althanstraße 14, A-1090 Wien, Austria [151]
EDWARDS, Amy Lyn, Museum of Natural History, University of Georgia, Athens, Georgia 30602, U.S.A. [126]
EGLOFF, D.A., Department of Biology, Oberlin College, Oberlin, Ohio 44074, U.S.A. [164]
EMERSON, William K., Department of Invertebrates, American Museum of Natural History, New York, NY 10024, U.S.A. [98, 155, 164, 165]
EMMETT, B., Archipelago Marine Research, #10, 1140 Fort Street, Victoria, British Columbia, V8L 3S1, Canada [123]
ETTER, Ron J., Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, U.S.A. [149]
EVERSOLE, Arnold G., Department of Aquaculture, Fisheries and Wildlife, Clemson University, Clemson, South Carolina 29634-0362, U.S.A. [126]
FABREGAS, J., Departamento de Microbiología, Facultad de Farmacia, Universidad de Santiago do Compostela, Spain [116]
FAINZILBER, Mike, Israel Oceanographic & Limnological Research, P.O. Box 8030, 31 080 Haifa, Israel [108, 133, 134, 138, 140, 141, 143-147]
FALKNER, Gerhard, Institut für Paläontologie und historische Geologie der Universität München, Richard-Wagner-Straße 10/II, 8000 München 2, F.R. Germany [113, 114, 115]
FALKNER, Margrit, Raiffeisenstraße 5, 8059 Hörlkofen, F.R. Germany [113]
FALNIOWSKI, Andrzej, Zoological Museum, Institute of Zoology, Jagiellonian University, ul. M. Karasia 6, 30-060 Kraków, Poland [110, 153]
FANG, Jianguang, Hwanghai Fisheries Institute, National Bureau of Aquatic Products, China [162]
FARFAN, Blanca Claudia, Centro de Investigacion Cientifica y de Educacion Superior de Ensenada (C.I.C.E.S.E.), Apartado Postal 2732, Ensenada, Baja California, 22830, Mexico [165]
FARMAKIS, N., Section of Statistics, Department of Mathematics, University of Thessaloniki, 540 06 Thessaloniki, Greece [120]
FARMER, Wesley M., 3591 Ruffin Road, No. 226, San Diego, California 92123, U.S.A. [165]
FARNETI, Marco, Instituto di Zoologia, dell'Università di Bologna, Italy [122]
FARRELL, Terrence M., Hopkins Marine Station, Stanford University, Pacific Grove, California 93950, U.S.A. [172]
FAUER, Wolfgang, Winterstein 24, 8561, Simmelsdorf, F.R. Germany [113]
FAUTIN, Daphne Gail, Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [165]
FERNANDES, Francisco, Cx.P. 12427, Luanda, Republic of Angola [107, 118]
FERNANDEZ, C., Dpto. de Biologia de Organismos y Sistemas, Universidad de Oviedo, 33005 Oviedo, Spain [119]
FERNANDEZ, E., Dpto. de Biologia de Organismos y Sistemas, Universidad de Oviedo, 33005 Oviedo, Spain [119]
FERNANDEZ, Guillem, C/. Concòrdia, 12, 08004 Barcelona, Spain [117]
FINET, Yves, Museum d'Histoire Naturelle, Case Postale 434, CH-1211 Geneve 6, Switzerland [172]
FISHER, T.W., Division of Biological Control, University of California, Riverside, California, U.S.A. [145]
FITT, William, Department of Zoology, University of Georgia, Athens, Georgia 30602, U.S.A. [171]
FLACH, E.C., Systematic Zoology Section, Leiden University, c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands [102]
FLESSA, Karl W., Department of Geosciences, University of Arizona, Tucson, Arizona 85721, U.S.A. [171]
FORCART, Lothar, Zürcher Straße 9, CH-4052 Basel, Switzerland [133, 140]
FORD, Susan E., Department of Oyster Culture, New Jersey Agricultural Experiment Station, Cook College, Rutgers University, Shellfish Research Laboratory, P.O. Box 687, Port Norris, New Jersey 08349, U.S.A. [122, 124]
FORSYTHE, John W., Marine Biomedical Institute, University of Texas Medical Branch, 200 University Boulevard, Galveston, Texas 77550-2772, U.S.A. [148]
FRANK, Christina, Josefstädterstraßr 64/11, A - 1080 Wien, Austria [99, 113, 114, 151, 153, 159, 160]
FRETTER, V., Department of Pure and Applied Zoology, University of Reading, U.K. [151]
FÜKÖH, Levente, Mátra Muzeum, Gyöngyös, Kossuth u. 40, H-3200, Hungary [158]

FULLER, S. Cynthia, Department of Zoology, Rutgers University, New Brunswick, New Jersey 08903, U.S.A. [149]
FURSICH, Franz T., Fachbereich Geowissenschaften, Universitat Bremen, D-2800 Bremen 33, West Germany [171]
GAL, Bruria, Kibbutz Lahav, Israel [141]
GARCIA, E.F., University of Southwestern Louisiana, Lafayette, LA 70504, U.S.A. [98]
GARCIA, F.J., Departamento de Zoología, Facultad de Biología, Univ. Sevilla, Ap. 1095, Reina Mercedes s/n. 41012 Sevilla, Spain [149]
GARCIA-GOMEZ, J.C., Departamento de Zoología, Facultad de Biología, Univ. Sevilla, Ap. 1095, Reina Mercedes s/n. 41012 Sevilla, Spain [117, 149]
GARDNER, Sandra M., Research Associate, Department of Biological Sciences, San Jose State University, San Jose, California 95192, U.S.A. [172]
GAT, Gil, Mollusc Collection, Zoological Museum, Hebrew University of Jerusalem, Israel [138-141, 144, 146, 147]
GEISEL, Kurt A., Hasharon Street 30A, Haifa, Israel [130, 132]
GEMMELL, Joyce, Department of Marine Invertebrates, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112, U.S.A. [171, 172]
GERBERICH, Andrew G., Division of Fishes, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A. [155]
GERMAIN, L., Collectif de Bio-écologie, Faculté des Sciences, Université libre de Bruxelles, 50, Av. F.D. Roosevelt, 1050 Brussels, Belgium [97, 98]
GHISELIN, Michael T., California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [172]
GHISOTTI, Fernando, Società Italiana di Malacologia, Viale Gadio, 2 - 20121 Milano (MI), Italy [104, 105]
GIANNUZZI-SAVELLI, Riccardo, Via Mater Dolorosa 54, 90146 Palermo, Italy [104]
GIBBONS, M.C., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062 [122]
GILLESPIE, David M., Marine Extension Service, University of Georgia, P.O. Box 13687, Savannah, Georgia 31416-0687, U.S.A. [124]
GITTENBERGER, E., Systematic Zoology Section, Leiden University, c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands [102, 103]
GIUSTI, Folco, Dipartimento di Biologia Evolutiva, Università di Siena, Via Mattioli 4, I-53100 Siena, Italy [104, 105]
GOFAS, Serge, Elf-Aquitaine, 64018 Pau, Paris, France [118]
GOLIKOV, A.N., Laboratory of Marine Investigation, Zoological Institute, USSR Academy of Sciences, University Embankment, 199164 Leningrad, 1, U.S.S.R. [150]
GOMEZ, Benjamin J., Laboratorio de Zoología, Dpto. de Biología, Facultad de Ciencias, Universidad del País Vasco, Aptdo. 644, 48080 Bilbao, Spain [100, 117]
GONZALEZ, Laura P., Estación Costera de Investigaciones Marinas, Las Cruces, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile [123]
GORDON, Carla M., Oysterseed Cooperative Project, Department of Zoology, University of the West Indies, Mona, Kingston 7, Jamaica [126]
GORDON, Mark E., Department of Zoology, University of Arkansas, Fayetteville, AR 72701, U.S.A. [155]
GOSLINER, Terrence M., Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [165, 166, 171]
GRACIO, Maria Amélia A., Instituto de Higiene e Medicina Tropical, R. Junqueira, 96, 1300 Lisboa, Portugal [150]
GRAHAM, A., Department of Pure and Applied Zoology, University of Reading, U.K. [151]
GRAHAME, J., Department of Pure and Applied Biology, University of Leeds, Leeds LS2 9JT, England, U.K. [121]
GRANT, W.S., Department of Genetics, University of the Witwatersrand, Wits 2050, Republic of South Africa [148]
GRAVINA, Flavia, Museo Civico di Zoologia, Via U. Aldrovandi 18, 00197 Roma, Italy [104, 105, 106]
GREENWOOD, J.G., Zoology Department, University of Queensland, St. Lucia, Brisbane, 4067, Australia [165]
GREIFENEDER, D., August-Bebel Str. 65, D-7730 Villingen-Schwenningen, West Germany [97]
GRIFFITHS, C.L., Zoology Department and Marine Biology Research Institute, University of Capetown, Rondebosch 7700, South Africa [119]
GRISOLI, Randall M., Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70148, U.S.A. [122]
GRIZZLE, Raymond E., Jackson Estuarine Laboratory, University of New Hampshire, Adams Point Road, Durham, New Hampshire 03824, U.S.A. [126]

GROSSU, A.V., 70731 Stirbei Voda 2, Ap. 7, Bucarest, Romania [97]
GROVE, Jack S., Section of Fishes, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. [172]
GRUET, Yves, Laboratoire de Biologie marine, Faculté des Sciences et Techniques 2, rue de la Houssinière, 44 072 Nantes Cedex 03, France [111]
GU, Jinrong, Institute of Parasitic Diseases, China National Centre for Preventive Medicine, China [161]
GUAN, Futian, Fisheries Research Institute of Yantai City, China [161]
GUERRA, A., Centro Experimental de Vilaxoán, Consellería de Pesca, Xunta de Galicia, Apdo. 208, Villagarcía Arosa, Spain [116]
GUISADO, Chita, Estación Costera de Investigaciones Marinas, Las Cruces, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile [123]
GUO, Shimao, Nanhai Fisheries Institute, China [162]
GUO, Yuanhua, Institute of Parasitic Diseases, China National Centre for Preventive Medicine, China [161]
HAAKER, Peter L., California Department of Fish and Game, 1301 W. 12th Street, Long Beach, California 90813, U.S.A. [171]
HABE, Tadashige, Natural History Museum, Tokai University, Miho, Shimizu, 424, Japan [167, 168, 169]
HABERLEHNER, Elisabeth, Limnologisches Institut der Universität Wien, Althanstraße 14, A-1090 Wien, Austria [114]
HABERMEHL, Gerhard, Regierung v. Mittelfranken, Schloß, 8800 Ansbach, F.R. Germany [114]
HACKNEY, C.R., Department of Food Science, Virginia Polytechnic Institute & State University, Blacksburg, Virginia 24061, U.S.A. [126]
HAIMOVICI, Manuel, Oceanography Department, Fundacão Universidade Do Rio Grande, Cx.P. 474, CEP 96.200, Rio Grande, Rs., Brazil [96]
HALDEMANN, Robert, Brückenstraße 71, Rüdersdorf, 1253, D.R. Germany [152]
HAMANN, Jeffrey C., 475 W. Bradley Avenue, El Cajon, California 92020, U.S.A. [165]
HAMMERSCHMIDT, Paul C., Texas Parks and Wildlife Department, Coastal Fisheries Branch, 4200 Smith School Road, Austin, Texas 78744, U.S.A. [122]
HANGAR, Rex Alan, Department of Paleontology, University of California, Berkeley, California 94720, U.S.A. [172]
HANKS, James E., Milford Laboratory, Milford, Connecticut, U.S.A. [123]
HANLON, Roger T., Marine Biomedical Institute, University of Texas Medical Branch, 200 University Boulevard, Galveston, Texas 77550-2772, U.S.A. [148]
HARASEWYCH, M.G., Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A. [126, 155, 166]
HARGIS, William J., Jr., Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [125]
HARMAN, Robert F., Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822, U.S.A. [148]
HARTWICK, E.B., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada [148]
HASKIN, Harold H., Department of Oyster Culture, New Jersey Agricultural Experiment Station, Cook College, Rutgers University, Shellfish Research Laboratory, P.O. Box 687, Port Norris, New Jersey 08349, U.S.A. [124]
HASZPRUNAR, Gerhard, Institut für Zoologie, Universität Innsbruck, Technikerstraße 25, A-6020 Innsbruck, Austria [119, 121, 151]
HAUSDORF, Bernhard, Tannenstraße 3, D-8504 Stein, F.R. Germany [115]
HAVEN, Dexter S., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [123, 125]
HAWKINS, C.M., Department of Fisheries and Oceans, Biological Sciences Branch, Scotia-Fundy Region, Halifax Fisheries Research Laboratory, P.O. Box 550, Halifax, Nova Scotia B3J 2S7, Canada [123]
HAYAMI, Itaru, Geological Institute, University of Tokyo, Tokyo 113, Japan [169]
HAYASAKA, Steven, Department of Microbiology, Clemson University, Clemson, South Carolina 29634-1909, U.S.A. [124]
HAYASHI, Ikuo, Ocean Research Institute, University of Tokyo, Minamidai 1-15-1, Nakano-ku, Tokyo 164, Japan [169]
HAYNES, A., School of Pure and Applied Sciences, University of the South Pacific, P.O. Box 1168, Suva, Fiji [164]
HE, Jinjin, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
HE, Ling, Shanghai Fisheries College, China [162]
HE, Lixuan, Nanhai Fisheries Institute, China [162]

HE, Xiuying, Beihai Farm of Pearl Culture, Guangxi Province, China [163]
HE, Yichao, Institute of Oceanology, Academia Sinica, China [161, 162]
HEALY, John M., Zoology Department, University of Queensland, St. Lucia, Queensland, Australia [121, 151]
HEFFERNAN, Peter B., Marine Extension Service, University of Georgia, P.O. Box 13687, Savannah, Georgia 31416-0687, U.S.A. [124]
HEIMAN, Eduard, David Elroi St. 12/29, 75303 Rishon Le Zion, Israel [144]
HEINEMANN, Helmut & Hanna, Wiesenweg 7, D-8359 Schöllnach, F.R. Germany [138, 141]
HENDERSON, Kristine, California Department of Fish and Game, 1301 West 12th Street, Long Beach, California 90813, U.S.A. [171]
HERGUETA, Eduardo, Departamento de Zoología, Facultad de Ciencias, Universidad de Málaga, 29071 Málaga, Spain [116]
HERRERO, C., Departamento de Microbiología, Facultad de Farmacia, Universidad de Santiago de Compostela, Spain [116]
HERRY, Angéle, Laboratoire de Zoologie, Université de Bretagne Occidentale, 29287 Brest Cédex, France [112, 126]
HERSHBERGER, William, College of Fisheries, University of Washington, Seattle, Washington 98195, U.S.A. [123]
HERSHLER, Robert, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A. [150]
HERTZ, Carole M., Department of Marine Invertebrates, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112, U.S.A. [171, 172]
HESLINGA, Jerry, [no address given] [136]
HETZEL, Erich W., P.O. Box HM2091, Hamilton #5, Bermuda [123]
HEUSS, Klaus, Promenade 27, 8800 Ansbach, F.R. Germany [114]
HICKMAN, Carole S., Department of Paleontology, University of California, Berkeley, California 94720, U.S.A. [151]
HIDU, Herbert, Department of Animal and Veterinary Sciences, Ira C. Darling Center, University of Maine, Walpole, Maine 04573, U.S.A. [124]
HINZ, W., Universität - Gesamthochschule - Duisburg, Fachbereich 6, Zoologie, Lotharstraße 65, D - 4100 Duisburg 1 (BRD), F.R. Germany [154]
HOCHBERG, F.G., Jr., Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105, U.S.A. [148, 166]
HODGSON, C.A., Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada [126]
HOENSELAAR, H.J., Zoölogisch Museum, P.O. Box 4766, 1009 AT Amsterdam, The Netherlands [102]
HOESE, H. Dickson, Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70507, U.S.A. [123]
HOFFMAN, James E., Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A. [164]
HOFSTETTER, R., Route 1, 4831 Elm Street, Seabrook, Texas 77586, U.S.A. [126]
HOLDENRIEDER, Ottmar, Auenstraße 6, 8050 Freising, F.R. Germany [114]
HOLLAND-BARTELS, L.E., U.S. Fish and Wildlife Service, National Fisheries Research Center, P.O. Box 818, La Crosse, Wisconsin 54602-0818, U.S.A. [150]
HOLYOAK, Alan R., Institute of Marine Sciences, University of California, Santa Cruz, California 95064, U.S.A. [164, 165]
HOMMAY, Gérard, Station de Zoologie, INRA, 28 rue de Herrlisheim, B.P. 507, 68021 Colmar cédex, France [111]
HONG-CHANG, Yaun Department of Epidemiology, School of Public Health, Shanghai Medical University, Shanghai, Peoples Republic of China [149]
HORTON, Howard, Department of Fisheries and Wildlife, Mark O. Hatfield Marine Science Center, Oregon State University, Newport, Oregon 97365, U.S.A. [123]
HORZEPA, George, Division of Water Resources, New Jersey Department of Environmental Protection, Trenton, New Jersey 08625, U.S.A. [125]
HOUART, Roland, Inst. Royal des Sciences Naturelles de Belgique, St. Jobsstraat, 8, B-3330 Landen (Esemaal), Belgium [97, 98, 168]
HOUBRICK, Richard S., National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A. [151]
HSIA, Kou-chin, Institute of Zoology, National Taiwan University, Taipei, Taiwan 10764, Republic of China [108]
HUANG, Baoyu, Nanjing Institute of Geology and Paleontology, Academia Sinica, China [162, 163]
HUANG, Qiuming, Zhanjian Fisheries College, China [163]
HUANG, Shuisheng, Institute of Parasitic Diseases, Hupei Academy of Medical Sciences, China [162]
HUANG, Weixun, Sanitary and Anti-epidemic Station of Changyang County, China [161]

HUANG, Yiming, Department of Biology, Fujian Teachers University, China [162]
HUANG, Yuesheng, Zhanjian Fisheries College, China [163]
HUART, D., Collectif de Bio-écologie, Faculté des Sciences, Université libre de Bruxelles, 50, Av. F.D. Roosevelt, 1050 Brussels, Belgium [99]
HUBBARD, E. Jane Albert, Kewalo Marine Laboratory, Pacific Biomedical Research Center, University of Hawaii, 41 Ahui Street, Honolulu, HI 96813 U.S.A. [121]
HUELSENBECK, J.P., Department of Paleontology, University of California, Berkeley, California 94720, U.S.A. [172]
HUEN, Juenchao, Zhejiang Fisheries Institute, China [162]
HUGHES, Roger N., School of Animal Biology, University College of North Wales, Bangor, Gwynedd LL57 2UW, U.K. [164]
HURLEY, Geoffrey V., Hurley Fisheries Consulting, P.O. Box 3049, East Postal Station, Dartmouth, Nova Scotia, B2W 4Y2, Canada [148]
IBAÑEZ, Miguel, Departamento de Zoología, Facultad de Biología, Universidad de La Laguna, Tenerife, Islas Canarias, Spain [100, 116]
IM, Seung-Kyun, Department of Parasitology, College of Medicine, Yonsei University, Seoul, Korea [127]
INOUE, Ryoko, Tokyo University of Fisheries, 4-5-7, Konan, Minato-ku, Tokyo 108, Japan [168]
ITOW, Syuzo, Nagasaki University, Nagasaki 852, Japan [172]
JABLONSKI, David, Department of the Geophysical Sciences, Univesity of Chicago, Chicago, Illinois 60637, U.S.A. [171]
JACKIEWICZ, Maria, Uniwersytet A. Mickiewicza, Zaklad Taksonomii i Ekologii Zwierzat, ul. Szamarzewskiego 91, 60-569 Poznan, Poland [153]
JAKLIN, A., Ruder Boskovic Institute, Rovinj, Yugoslavia [119]
JAMES, Matthew J., Department of Geology, Sonoma State University, Rohnert Park, California 94928, U.S.A. [171, 172]
JANOWSKY, Robert, [no address given] [135]
JANSSEN, A.W., Rijksmuseum van Geologie en Mineralogie, Hooglandse Kerkgracht 17, 2312 HS Leiden, The Netherlands [103]
JANSSEN, R., [address not given] [100]
JARAI, József, Baja, Rudnay u.19, H-6500, Hungary [159]
JIANG, Jinxiang, Third Institute of Oceanography, National Bureau of Oceanography, China [162]
JIANG, Weiguo, South China Sea Institute of Oceanology, Academia Sinica, China [161]
JOHNSON, Lisa, Department of Microbiology, Clemson University, Clemson, South Carolina 29634-1909, U.S.A. [124]
JOLL, L.M., Western Australian Marine Research Laboratories, P.O. Box 20, North Beach 6020, Western Australia [124]
JONES, G.W., Dept. of Zoology, University College Cardiff, Cardiff CF1 1XL, Wales, U.K. [121]
JONES, R.H., [no address given] [134]
JOUNG, In-Sil, Department of Parasitology, College of Medicine, Yonsei University, Seoul, Korea [127]
JUNG, Younghun, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A. [128, 170]
KAAS, Piet, Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands [103]
KABAT, Alan R., Department of Mollusks, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A. [156]
KANALEY, Sheila A., Shellfish Research Laboratory, New Jersey Agricultural Experiment Station, Cook College, Rutgers University, Port Norris, New Jersey 08349, U.S.A. [124]
KANTOR, Yu.I., A.N. Severtzov Institute of Animal Evolutionary Morphology and Ecology of the USSR Academy of Sciences, Lenin Avenue 33, Moscow 117071, U.S.S.R. [99]
KARMON, Nira, Center for Maritime Studies, University of Haifa, Israel [136, 139]
KASSNER, Jeffrey, Town of Brookhaven, Division of Environmental Protection, 3233 Route 112, Medford, New York 11763, U.S.A. [125]
KEESING, John K., Western Australian Museum, Perth 6000, Western Australia [119]
KEITHLY, Walter R., Jr., Center for Wetland Resources, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A. [126]
KELLOGG, Michael G., Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [165]
KEMPERMAN, Th.C.M., Systematic Zoology Section, Leiden University, c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands [102]
KERSTITCH, Alex, 10700 E. Calle Vaqueros, Tucson, Arizona 85749, U.S.A. [164]
KIERDORF-TRAUT, Georg, Weißes Haus, 4402 Greven-Gimbte, F.R. Germany [114]

KILGEN, Marilyn B., Department of Biological Sciences, Nicholls State University, Thibodaux, Louisiana 70310, U.S.A. [126]
KIM, B.S., Department of Preventive Medicine, Dong-A Medical College, Pusan, Korea [127]
KIM, Chang Han, Department of Science Education, Chungbuk National University, Korea [127]
KIM, J.Y., Department of Preventive Medicine, Dong-A Medical College, Pusan, Korea [127]
KIM, Jae Jin, Department of Biology, College of Science, Yonsei University, Seoul, Korea [128]
KIM, S.C., Department of Preventive Medicine and Institute of Industrial Medicine, Inje College, Pusan, Korea [127]
KIM, Sung-Soon, National Institute of Health, Korea [128]
KIRBY, G.C., School of Biological Sciences, Flinders University, Bedford Park, South Australia, 5042 Australia [121]
KISS, Éva, Természettudományi Muzeum ´Allattára, Budapest, Baross u. 13, H-1088, Hungary [158, 159, 160]
KISS, János Botond, 8800 Tulcea Of.p.4., str.23.August Nr.167, Sc.A, Ap.3., R.P. Romania [158]
KITTING, Christopher L., Department of Biological Sciences, California State University, Hayward, California 94542, U.S.A. [172]
KLEIN, Dominique, Laboratoire de Zoologie générale et d'Ecophysiologie (L.A. INRA), Université de Rennes I, Campus de Beaulieu, Avenue de Général Leclerc, 35042 Rennes Cedex, France [112]
KNAUB, Richard S., Aquaculture Research Center, Kentucky State University, Frankfort, Kentucky 40601, U.S.A. [126]
KNIGHT, Ron, P.O. Box 108, Lorengau, Manus, Papua New Guinea [146]
KOMATSU, Shigemi, Mukaishima Marine Biological Station of Hiroshima University, Mukaishima-cho, Hiroshima-ken 722, Japan [169]
KONDO, Takaki, Department of Biology, Osaka Kyoiku University, Osaka 543, Japan [168]
KOOL, Silvard P., Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560, U.S.A. [149]
KÖRNIG, Gerhard, Pestalozzistraße 54, Halle (S.), 4020, D.R. Germany [152]
KOSUGE, Sadao, Institute of Malacology of Tokyo, 6-36, Midoricho 3 chome, Tanashi City, Tokyo 188, Japan [107, 157]
KRAEUTER, John N., Crane Aquaculture Facility, Baltimore Gas and Electric, P.O. Box 1475, Baltimore, Maryland 21203, U.S.A. [122]
KRAUS, Richard A., Aquacultural Research Corporation, P.O. Box AC, Dennis, Massachusetts 02638, U.S.A. [123]
KROLOPP, Endre, Magyar ´Allami Földtani Intézet, Budapest, Népstadion-ut 14, H-1143, Hungary [158]
KUEHL, Silke, Alfred-Wegener-Institut für Polarforschung, Columbus-Center, D-2850 Bremerhaven, F.R. Germany [148]
KUIJPER, W.J., Instituut voor Prehistorie, Rijksuniversiteit Leiden, Postbus 9515, 2300 RA Leiden, The Netherlands [103]
KUIPER, J.G.J., c/o Institut Néerlandais, 121 rue de Lille, F - 75007 Paris, France [154, 159]
KURIS, Armand M., Department of Biological Sciences, University of California, Santa Barbara, California 93106, U.S.A. [165]
KWON, Oh-Kil, Department of Biology, Kangweon National University, Korea [127]
LABORDA NAVIA, Antonio José, Departamento de Biología Animal, Facultad de Biología, Universidad de León, 27071 León, Spain [116]
LAI, Kin-yang, Taiwan Museum, No. 2 Siang-Yang Road, Taipei, Taiwan, Republic of China [108]
LAM, P.K.S., Department of Biology, King's College London (KQC), Campden Hill Road, London W8 7AH, England, U.K. [120, 121]
LAMBERT, Marie Cécile, Laboratoire de Zoologie générale et d'Ecophysiologie (L.A. INRA), Université de Rennes I, Campus de Beaulieu, Avenue de Général Leclerc, 35042 Rennes Cedex, France [111]
LAMOTTE, Maxime, Ecole Normale Supérieure, Laboratoire de Zoologie, 46 rue d'Ulm, 75230 Paris Cedex 05, France [111]
LAN, Xiu, Nanjing Institute of Geology and Paleontology, Academia Sinica, China [162]
LANDAU, Matthew, Department of Molecular and Cell Biology, University of Connecticut, Storrs, Connecticut 06268, U.S.A. [122]
LANGWAY, L., [no address given] [134]
LAUTIÉ, Nicole, Laboratoire d'Histophysiologia Fondamentale et Appliquée, Unité Associée au C.N.R.S. No. 680, Université Pierre et Marie Curie, 12 rue Cuvier, 75005 Paris, France [149]
LAVENIR, Jean Eric, "La Roquetaillant", Ventabren 13122, France [144]
LAWTON, Peter, Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, New York 11794-5000, U.S.A. [126]
LAZARIDOU-DIMITRIADOU, M., Section of Zoology, Department of Biology, University of Thessaloniki, 540 06 Thessaloniki, Greece [120]

LEE, C.U., Department of Preventive Medicine and Institute of Industrial Medicine, Inje College, Pusan, Korea [127]
LEE, Harry G., 709 Lomax Street, Jacksonville, Florida 32204, U.S.A. [134, 136, 156]
LEE, J.T., Department of Preventive Medicine and Institute of Industrial Medicine, Inje College, Pusan, Korea [127]
LEE, Jun-Sang, Department of Biology, Kangweon National University, Korea [127]
LEE, Keun-Tae, Department of Parasitology, College of Medicine, Yonsei University, Seoul, Korea [127]
LEE, S.Y., Department of Zoology, The University of Hong Kong, Hong Kong [121]
LEEHMAN, Elmer G., [no address given] [135]
LEIGHTON, Bruce J., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada [165]
LEIGHTON, David L., Department of Natural Science, San Diego State University, San Diego, California, U.S.A. [171]
LE PENNEC, Marcel, Laboratoire de Zoologie, Université de Bretagne Occidentale, 29287 Brest Cédex, France [112, 126]
LE ROUX, F.G., Geological Survey, P.O. Box 1774, Port Elizabeth 6000, South Africa [164]
LEVER, A.J., Centre for Agricultural Publishing and Documentation (PUDOC), Generaal Foulkesweg 19, P.O. Box 4, 6700 AA Wageningen, The Netherlands [103]
LE VOCI, G., Dipartimento di Biologia Animale e Genetica, Università degli Studi di Firenze, Via Romana 17, 50125 Florence, Italy [120]
LI, Fenglan, Institute of Oceanology, Academia Sinica, China [161]
LI, Hengde, Fisheries Technical Extensive Station of Honghu, Hubei Province, China [162]
LI, Qingyi, Department of Biology, Southwest China Teachers College, China [161]
LI, Rongguan, Third Institute of Oceanography, National Bureau of Oceanography, China [162]
LI, Shuying, Institute of Oceanology, Academia Sinica, China [161]
LI, Suqin, Human Institute of Parasitic Disease Control, China [162]
LI, Yongfang, South China Sea Fisheries Research Institute, China [162]
LI, Yuntong, Institute of Geology, Chinese Academy of Geological Sciences, China [163]
LIANG, Guangyue, Guangxi Marine Fisheries Institute, China [162]
LIANG, Xianyuan, Department of Biology, Zhongshan University, China [162]
LIGHT, Janice M., 88 Peperharow Road, Godalming, Surrey, GU7 2PN, England, U.K. [118]
LILTVED, William R., Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [164]
LIN, Bishui, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
LIN, Faxiang, Minhou Technological Station of Fishery, Fujian Province, China [163]
LIN, Han, Department of Aquaculture, National Taiwan College of Marine Science and Technology, Keelung, Republic of China [108]
LIN, Huiqiong, Fujian Institute of Oceanology, China [162]
LIN, Tien-Shang, Institute of Zoology, Academia Sinica, Taipei, Taiwan 11529, Republic of China [108]
LIN, Xiuying, Department of Biology, Fujian Teachers University, China [162]
LINDBERG, David R., Museum of Paleontology, University of California, Berkeley, California 94720, U.S.A. [151, 164]
LINDER, Elisha, Center for Maritime Studies, University of Haifa, Israel [139]
LISICKY, Mikulás J., Ustav Experimentálnej, Biológie a Ekológie SAV, Bratislava, Ul.obrancov Mieru 3, OSSR-814 34, Czechoslovakia [160]
LITTLEWOOD, D. Timothy J., Oysterseed Cooperative Project, Department of Zoology, University of the West Indies, Mona, Kingston 7, Jamaica [126]
LIU, Hsiu-ping, Institute of Fishery Sciences, National Taiwan University, Taipei, Taiwan 10764, Republic of China [108]
LIU, Tudi, Minhou Shell and Straw Farm of Xiangqian County, China [163]
LIU, Xiangsheng, Institute of Oceanology, Academia Sinica, China [161, 162]
LIU, Yuan, Department of Biology, Zhongshan University, China [162]
LIU, Yueying, Institute of Zoology, Academia Sinica, China [161, 163]
LOOSJES, F.E., Vossenlaan 4, NL 6705 CE Wageningen, The Netherlands [103]
LOOSJES-VAN BEMMEL, A.C.W., Vossenlaan 4, NL 6705 CE Wageningen, The Netherlands [103]
LOPEZ ESTRADA, Eduardo, Dept. Anthropologie, Université Laval, Québec, Canada [125]
LORENZ, Felix, jun., Ginsterweg 6, 2058 Lauenburg, F.R. Germany [114]
LOU, Kanghou, Institute of Oceanology, Academia Sinica, China [163]
LOUVET, Murielle, Laboratoires de Morphologie, Systématique et Ecologie animales (Prof. Ch. Jeuniaux), Institut de Zoologie, Université de Liège, 22, Quai van Neneden, B-4020 Liege, Belgium [112]

LOZEK, V., Institut für Geologie und Geotechnik der Akademie der Wissenschaften der CSSR, Navrátilova 12, CS - 110 00 Praha 2 Czechoslovakia [154]
LU, Daijun, Fisheries Technical Extensive Station of Honghu, Hubei Province, China [162]
LÜ, Duanhua, Institute of Oceanology, Academia Sinica, China [161]
LU, Weiping, Shanghai Fisheries College, China [162]
LU, Yunfang, Institute of Parasitic Diseases, Hupei Academy of Medical Sciences, China [162]
LUIZ dos SANTOS CRUZ, Renato, Department de Zoologia, Instituto de Biologia, C.C.S., Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro, 21940, Brasil [155]
LUQUE, Angel A., Departamento de Zoologia, Facultad de Ciencias, Universidad Autónoma, 28049, Madrid, Spain [120, 151]
LUTZ, Richard A., Department of Oyster Culture, Rutgers University, New Brunswick, New Jersey 08903, U.S.A. [126, 149]
MA, Enbo, Department of Biology, Shanxi University, China [162]
MA, Jianghu, Institute of Oceanology, Academia Sinica, China [161, 162]
MA, Junling, Freshwater Fisheries Institute of Shandong Province, China [161]
MA, Xiutong, Institute of Oceanology, Academia Sinica, China [161]
MAAROUF, A.M., Laboratoire d'Ecologie, 1 Rue des Récollets, 57000 Metz, France [112]
MACALUSO, M., Institute of Zoology, University of Palermo, Via Archirafi 18 -- 90123 Palermo, Italy [149]
MACKENZIE, Clyde L., Jr., U.S. National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook Laboratory, Highlands, New Jersey 07732, U.S.A. [122]
MAEDA, Toyohide, Laboratory of Fish Culture, Tokyo University of Fisheries, 5-7, Konan-4, Minato-ku, Tokyo 108, Japan [169]
MAILLARD, Yves, Laboratoire de Biologie marine, Faculté des Sciences et Techniques 2, rue de la Houssinière, 44 072 Nantes Cedex 03, France [111]
MAJOROS, Gábor, Budapest, Thököly ut 25.I/5, H-1076, Hungary [160]
MALACHOWSKI, Mark, Humboldt State University, Marine Laboratory, Trinidad, California 95570, U.S.A. [126]
MALINOWSKI, Steve M., The Clam Farm, Inc., P.O. Box 402, Fishers Island, New York 06390, U.S.A. [126]
MALINOWSKI, Steven, Department of Marine Sciences, University of Connecticut, Avery Point, Groton, Connecticut 06340, U.S.A. [124]
MANGA-GONZALEZ, Ma. Yolanda, Estación Agrícola Experimental (C.S.I.C.), Ap. 788, 24080 León, Spain [118]
MANGANELLI, Giuseppe, Dipartimento di Biologia Evolutiva, Università di Siena, Via Mattioli 4, I-53100 Siena, Italy [104]
MANGOLD, Katharina, Laboratoire Arago, 66650 Banyuls-sur-Mer, France [148]
MANN, Roger, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [122, 124, 126]
MARIN, Arnaldo, Departamento de Ecología, Facultad de Biología, Universidad de Murcia, 30071 Murcia, Spain [116]
MARINONI, Morag, c/o S.A.P.L., Construction - Public Works, P.O. Box 167, Yanbu, Saudi Arabia [141]
MARIOTTINI, Paolo, Dip. di Biologia, II Università di Roma, Via O. Raimondo, 00173 Roma, Italy [104, 105, 106]
MARQUET, R., Rijksuniversitair Centrum Antwerpen, Laboratorium voor Algemene Dierkunde, Groenenborgerlaan, 171, B-2020 Antwerp, Belgium [98]
MARRIOTT, R.W. & Dorothy K., 14 View Terrace, Aberdeen AB2 4RR, England, U.K. [118]
MARSHALL, B.A., National Museum of New Zealand, P.O. Box 467, Wellington, New Zealand [120]
MARTIN, P., 65, Rue Veydt, B-1050 Bruxelles, Belgium [98]
MARTIN, Ramón, Laboratorio de Zoología, Dpto. de Biología, Facultad de Ciencias, Universidad del País Vasco, Apdo. 644, 48080 Bilbao, Spain [100, 117]
MARTINEZ, Sergio, Departamento de Paleontología, Facultad de Humanidades y Ciencias, Tristán Narvaja 1674, Montevideo, Uruguay [109]
MARTINEZ-LOPEZ, F., Dpto. Zoología, Fac. C. Biológicas, Univ. Valencia; Dr. Moliner, 50 Burjasot 46100 Valencia, Spain [116]
MASELLO, Arianna, Sección Recursos Bentónicos, Instituto Nacional de Pesca (INAPE), Casilla de Correo 1612, Montevideo, Uruguay [109]
MATHER, Jennifer A., Department of Psychology, University of Lethbridge, Lethbridge, Alberta, T1K 3M4, Canada [148]
MATZKE, Manfred, Pädagogische Hochschule, "N.K. Krupskaja" Halle, Sektion Biologie/Chemie, Kröllwitzer Straße 44, Halle (S.), 4050, D.R. Germany [154]
MAZE GONZALEZ, Raquel Ana, Departamento de Biología Animal, Facultad de Biología, Universidad de León, 27071 León, Spain [116]

McCARTHY, Kevin J., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [126, 166]
McCAY, Bonnie J., Department of Human Ecology, Cook College, Rutgers University, Port Norris, New Jersey 08349, U.S.A. [125]
McCLINTIC, D., [no address given] [146]
McGRAW, K.A., Seattle District Corps of Engineers, P.O. Box C-3755, Seattle, Washington 98124, U.S.A. [125]
McKINSTRY, Donald M., Division of Science, Engineering, and Technology, The Pennsylvania State University at Erie, The Behrend College, Erie, PA 16563-1200, U.S.A. [155]
McLEAN, James H., Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. [151, 155, 164, 172]
MEAD, Albert R., Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721, U.S.A. [121]
MENDL, Wolfgang, Lab. Acarología, Departamento Zoología, Escuela Nacional de Ciencias Biológicas, Apartado Postal 42186, México 11340, México [155]
MENKHORST, H.P.M.G., Natuurmuseum Rotterdam, P.O. Box 23452, 3001 KL Rotterdam, The Netherlands [102, 103]
MIENIS, Henk K., Zoological Museum, Mollusc Collection, Hebrew University, 91904 Jerusalem, Israel [108, 129-147, 160]
MILL, P.J., Department of Pure and Applied Biology, University of Leeds, Leeds LS2 9JT, England, U.K. [121]
MILLEN, Sandra, University of British Columbia, British Columbia, V6T 2A9, Canada [171]
MILLER, Walter B., Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A. [165]
MINATO, Hiroshi, Kumano Senior High School, Kamitonda-cho, Wakayama-ken, 649-21, Japan [169]
MOCQUARD, Jean-Pierre, Laboratoire de Physiologie et de Génétique des Crustacés, Université de Poitiers, ERA No. 230 UFR.SFA, 86022 Poitiers, France [111]
MOFFITT, Robert B., National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory, 2570 Dole Street, Honolulu, Hawaii 96822, U.S.A. [165]
MONTES, J., Centro Experimental de Vilaxoán, Consellería de Pesca, Xunta de Galicia, Apdo. 208, Villagarcía de Arosa, Spain [116]
MONTOYA, Michel, P.O. Box 6327, San Jose, Costa Rica [171]
MOOK, William, Mook Sea Farms, Damariscotta, Maine 04543, U.S.A. [124]
MOOLENBEEK, R.G., Zoölogisch Museum, P.O. Box 4766, 1009 AT Amsterdam, The Netherlands [102]
MOORE, Donald R., Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A. [156]
MORAGA, Dario, Laboratoire de Zoologie, Faculté des Sciences, 29287 Brest Cedex, France [112]
MORALES, Pedro, Departamento de Zoología, Facultad de Biología, Universidad de La Laguna, Tenerife, Islas Canarias, Spain [100]
MORALES-ALAMO, Reinaldo, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [126]
MORAND, Serge, Laboratoire de Zoologie et d'Ecophysiologie (L.A. INRA), Université de Rennes I, Campus de Beaulieu, 35042 Rennes Cedex, France [112, 120]
MORONI, Maria Antonietta, Dipartimento di Geologia e Geodesia della Università, Corso Tuköry 131, 90134 Palermo, Italy [106]
MORRIS, Noel J., British Museum of Natural History, Cromwell Road, London SW7 5BD, U.K. [151]
MORRONDO-PELAYO, Ma. Patrocinio, Estación Agrícola Experimental (C.S.I.C.), Ap. 788, 24080 León, Spain [119]
MORSE, Aileen N.C., Marine Science Institute, University of California, Santa Barbara, California 93106, U.S.A. [171]
MORTON, Brian, Department of Zoology, University of Hong Kong, Hong Kong [119, 120, 150, 172]
MOUABAD, A., Laboratoire d'Ecologie, 1 Rue des Récollets, 57000 Metz, France [112]
MOYA, Jesús, Apartado 644, Facultad de Ciencias, Universidad del Pais Vasco, Bilbao, Spain [115]
MOYER, Steven N., National Wildlife Federation, 1412 16th Street, N.W., Washington, D.C. 20036, U.S.A. [96]
MÜLLER, E.-Dieter, Institut für Paläontologie und historische Geologie der Universität München, Richard-Wagner-Straße 10/2, 8000 München 2, F.R. Germany [113, 114]
MULLINER, David K., San Diego Natural History Museum, San Diego, California 92112, U.S.A. [171]
MULVEY, Margaret, Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801, U.S.A. [149]
MYERS, Barbara W., Department of Marine Invertebrates, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112, U.S.A. [155, 171, 172]
MYLONAS, M., University of Athens, Department of Biology, Section of Ecology and Taxonomy, Panepistimioupolis, Ilissia, GR - 157 71 Athens, Greece [154]

NAIDU, K.S., Science Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland, A1C 5X1, Canada [124]
NARANJO-GARCIA, Edna, Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A. [165]
NÉMETH, László, Budapest, Rekettye u.24, H-1155, Hungary [159]
NESEMANN, Hasko, Bornstraße 73, 6238 Hofheim-Lorsbach, F.R. Germany [115]
NEVES, Richard J., Virginia Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, U.S.A. [96]
NEWELL, Roger I.E., Horn Point Environmental Laboratories, University of Maryland, P.O. Box 775, Cambridge, Maryland 21613, U.S.A. [122]
NEWMAN, L.J., Zoology Department, University of Queensland, St. Lucia, Brisbane, 4067, Australia [165]
NEWMAN, Michael C., Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801, U.S.A. [149]
NGOILE, M., Department of Zoology, University of Aberdeen, Scotland
NI, Haier, Zhejiang Fisheries Institute, China [162]
NIE, Zonqien, Hwanghai Fisheries Institute, National Bureau of Aquatic Products, China [162]
NINOMIYA, Taizo, 10-12 Himon-ya 2, Meguro-ku, Tokyo 152, Japan [167]
NISHIHAMA, Shiro, Amakusa Marine Biological Laboratory, Kyushu University, Tomioka, Reihoku, Amakusa-gun, Kumamoto-ken, 863-25, Japan [168]
NISTERS, Helmut, Franz-Fischer-Straße 46, A-6020 Innsbruck, Austria [114]
NOMBELA, M.A., Universidad de Santiago, Colegio Universitario, Apdo. 874, Vigo, Spain [116]
NOMURA, Tadashi, Department of Fishery Science, Faculty of Agriculture, Tohoku University, Tsutsumidori-Amamiyamachi, Sendai, 980, Japan [168]
NORDSIECK, Hartmut, Johannesstraße 38, 7730 Villingen-Schwenningen, F.R. Germany [113, 114, 115]
NORRIS, A., Department of Natural History, Leeds City Museums, LS1 3AA, England, U.K. [118]
NYBAKKEN, James, Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, California 95039, U.S.A. [166]
O'DOR, Ronald K., Biology Department and Aquatron Laboratory, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada [148]
O FOIGHIL, Diarmaid, Friday Harbor Laboratories, Friday Harbor, Washington 98250, U.S.A. [166]
OGAWA, Jogi, CINVESTAV IPN Mérida, A.P. 73 Cordemex, C.P. 97610, Mérida, Mexico [112]
OGLE, John T., Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, Mississippi 39564, U.S.A. [126]
OHNO, Yuriko, Department of Geoscience, Joetsu University of Education, Yamayashiki-cho, Joetsu City, Niigata Pref., 943, Japan [169]
OHTA, Suguru, Ocean Research Institute, University of Tokyo, Minamidai 1-15-1, Nakano-ku, Tokyo 164, Japan [169]
OKAMOTO, Masatoyo, 4-18-7, Tsukushigaoka, Kashiwa City, 277, Japan [167]
OKAMURA, Ichiro, 205, Masago-cho, Matsue City, 690, Japan [168]
OKOSHI, Kenji, Department of Fishery Science, Faculty of Agriculture, Tohoku University, Tsutsumidori-Amamiyamachi, Sendai, 980, Japan [168]
OKUTANI, Takashi, Tokyo University of Fisheries, 4-5-7, Konan, Minato-ku, Tokyo 108, Japan [167, 168, 169]
OLAZARRI, José, Investigador Asociado del Museo Nacional de Historia Natural de Montevideo, Rivas 687, Mercedes, Uruguay [109]
OLIVERIO, Marco, Via delle Sirene 56, 00121 Ostia Lido (Roma), Italy [106]
OLSON, Annette M., Department of Zoology, Oregon State University, Corvallis, Oregon 97331, U.S.A. [172]
O'NEILL, Susan, Department of Biology, University of Massachusetts, Boston, Massachusetts 02125, U.S.A. [149]
ONG, Wen-lian, Kinchen Junior High School, Kinmen, Republic of China [108]
ORR, J., [no address given] [133]
ORTEA, Jesús, Departamento de Zoología, Facultad de Ciencias Biológicas, Universidad de Oviedo, Oviedo, Spain [120]
ORTH, R.E., Division of Biological Control, University of California, Riverside, California, U.S.A. [145]
OSORIO, Cecilia, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile [164]
OTERO SCHMITT, J.J., Avenida de las Ciencias s/n. Santiago de Compostela, Spain [116]
OUTEIRO, Adolfo, Departamento de Biología Animal, Facultad de Biología, Universidad de Santiago de Compostela, Spain [117]

OWENS, Leigh, Graduate School of Tropical Veterinary Science, P.O. James Cook University of North Queensland, 4811, Australia [123]
OZINSKY, Sheryl, c/o Loon, 4a Watson St., Haifa, Israel [141]
PADILLA, Dianna K., Department of Entomology, Cornell University, Ithaca, New York, U.S.A. [172]
PAI, Jenn-yü, Institute of Zoology, National Taiwan University, Taipei, Taiwan 10764, Republic of China [108]
PAIK, N.W., Paik Medical Center, Inje College, Seoul, Korea [127]
PALAZZI, Stefano, Viale Moreali 4, 41100 Modena (Mo), Italy [106]
PALMER, A. Richard, Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada [166]
PALMERI, Alberto, Vicolo Parrini 10, 90145 Palermo, Italy [104]
PAN, Yuntang, Graduate School, Academia Sinica, China [162]
PANG, Jingliang, South China Sea Institute of Oceanology, Academia Sinica, China [163]
PANIGRAHI, A., Department of Zoology, Calcutta University, 35 Ballygunge Circular Road, Calcutta 700 019, India [105, 150]
PANTOLI, Deano, Via Bidente 30, 47100 Forlì, Italy [105]
PARACHE, Alain, Station Marine d'Endoume, 13007 Marseille, Station I.F.R.E.M.E.R., Quai du Commandant Silhouette, 33120 Arcachon, France [112]
PARK, Gap-Man, Department of Biology, Kangweon National University, Korea [127]
PARK, Sung-Bin, Department of Biology, Kangweon National University, Korea [128]
PARMALEE, Paul W., Frank H. McClung Museum, University of Tennessee, Knoxville, TN 37996, U.S.A. [96]
PARPAGNOLI, D., Dipartimento di Biologia Animale e Genetica, Università degli Studi di Firenze, Via Romana 17, 50125 Florence, Italy [120]
PAUL, C.R.C., Department of Earth Sciences, Liverpool University, L69 3BX, England, U.K. [118]
PAUSINA, Ralph, Pausina Oyster Corporation, New Orleans, Louisiana, U.S.A. [126]
PEDROSO, L.A., Investigador del Centro de Estudos Costeiros, Limnológicos e Marinhos (CECLIMAR) de la Universidad Federal de Río Grande do Sul, Uruguay [109]
PEKLI, József, Gödölló, Fácánsor 56, H-2100, Hungary [160]
PELED, Dov, [no address given] [136]
PEMBROKE, J.E., Department of Biology, Oberlin College, Oberlin, Ohio 44074, U.S.A. [164]
PEÑA, Juan B., Instituto de Acuicultura Torre de la Sal. (C.S.I.C.), Ribera de Cabanes, 12595 Castellón, Spain [116, 117]
PEÑA, Junkal, Sociedad Cultural INSUB, Museo de Oquendo, Apartado 3031, 20080 San Sebastián, Spain [116]
PENCHASZADEH, P.E., INTECMAR, Universidad Simón Bolívar, Apdo. 89.000, Caracas 1080, Venezuela [151]
PERDUE, James, College of Fisheries, University of Washington, Seattle, Washington 98195, U.S.A. [123]
PEREIRA, J., Investigador del Museo Oceanográfico de la FURG, Fundação Universidade de Rio Grande, RS, Uruguay [109]
PEREZ GANDARAS, G., Instituto Investigaciones Marinas, Bouzas, Vigo, Spain [116]
PERRET, William S., Louisiana Department of Wildlife and Fisheries, P.O. Box 98000, Baton Rouge, Louisiana 70898-9000, U.S.A. [125]
PETIT, Richard E., 806 St. Charles Road, North Myrtle Beach, South Carolina 29582, U.S.A. [155, 156, 164]
PETROVITS, Eugene J., Aquacultural Research Corporation, P.O. Box AC, Dennis, Massachusetts 02638, U.S.A. [123]
PEZZOLI, Enrico, Via Fornari 48, 20146 Milano, Italy [104]
PHELPS, Harriette L., University of the District of Columbia, 4200 Connecticut Ave. N.W., Washington, District of Columbia 20008, U.S.A. [123]
PIHAN, J.C., Laboratoire d'Ecologie, 1 Rue des Récollets, 57000 Metz, France [111, 112]
PINTÉR, László, Naturwissenschaftliches Museum, H-1088 Budapest, Baross utca 13, Hungary [130]
PISCITELLI, G., Istituto de Zoologia e Anatomia Comparata dell'Università di Bari, Italy [105]
PITT, Lois J., 2444 38th Ave., Sacramento, California 95822, U.S.A. [172]
PITT, William D., Department of Geology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [171, 172]
POIRRIER, Michael A., Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70148, U.S.A. [122, 123]
POLACO, Oscar J., Departamento de Prehistoria, Instituto Nacional de Antropología e Historia, Moneda #16, México 06060, México [155]
POMPONI, Shirley A., Harbor Branch Oceanographic Institution, Inc., 5600 Old Dixie Highway, Fort Pierce, FL 34946, U.S.A. [155]
PONDER, W.F., The Australian Museum, 6-8 College Street, Sydney, NSW, 2000, Australia [121, 151]

PONYI, Jenó, Tihany, MTA Limnol., Kut. Int., H-8237, Hungary [159]
POPHAM, J.D., Seakem Oceanography Ltd., 2045 Mills Road, Sidney, British Columbia, V8L 3S1, Canada [123]
POPPE, Guido T., Mortselveldenlaan 25 Bus 7, 2510 Mortsel, Belgium [97, 98, 169]
POULICEK, Mathieu, Laboratoires de Morphologie, Systématique et Ecologie animales (Prof. Ch. Jeuniaux), Institut de Zoologie, Université de Liège, 22, Quai van Neneden, B-4020 Liege, Belgium [112]
POWELL, Charles L., II, U.S. Geological Survey, M/S 915, 345 Middlefield Road, Menlo Park, California 94025, U.S.A. [171]
POWELL, E.N., Department of Oceanography, Texas A&M University, College Station, Texas 77843, U.S.A. [123, 165]
PREECE, R.C., Department of Zoology, University of Cambridge CB2 3EJ, England, U.K. [118]
PREZANT, Robert S., Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania 15705, U.S.A. [166]
PRIETO, C.E., Departamento de Biología Animal y Genética, Facultad de Ciencias. UPV/EHU. Apdo. 644. 48080 Bilbao, Spain [117]
PROSCHWITZ, T. von, Naturhistoriska Museet, Box 7283, S - 40235 Göteborg, Sweden [118, 154]
PUJANTE MORA, A., Dpto. Zoología, Fac. C. Biológicas, Univ. Valencia; Dr. Moliner, 50 Burjasot 46100 Valencia, Spain [116]
QI, Qiuzhen, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
QI, Zhongyan, Institute of Oceanology, Academia Sinica, China [161]
QIU, Liqiang, South China Sea Fisheries Research Institute, China [162]
QUINN, G.P., Department of Zoology, University of Melbourne, Parkville, Victoria, 3052, Australia [119]
RADOSH, David J., U.S. National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook Laboratory, Highlands, New Jersey 07732, U.S.A. [122]
RÄHLE, Wolfgang, Institut für Biologie III der Universität Tübingen, Auf der Morgenstelle 28, D-7400 Tübingen 1, West Germany [100]
RAMIREZ, L. Fernando Bückle, Centro de Investigacion Cientifica y de Educacion Superior de Ensenada (C.I.C.E.S.E.), Apartado Postal 2732, Ensenada, Baja California, 22830, Mexico [165]
RAMIREZ, M. Eliana, Sección Botánica, Museo Nacional de Historia Natural, Casilla 787, Santiago, Chile [164]
RAMOS, M.A., Museo Nacional de Ciencias Naturales, (C.S.I.C.), Jose Gutierrez Abascal 2, 28006 Madrid, Spain [121]
RATH, Elisabeth, Institut für Zoologie der Universität Wien, Althanstr. 14, A-1090 Wien, Austria [151]
RAUT, S.K., Department of Zoology, Calcutta University, 35 Ballygunge Circular Road, Calcutta 700 019, India [105, 150]
RAVEN, J.G.M., 2a Gilpin Avenue, East Sheen, London SW14 8QY, England, U.K. [102]
RAY, S.M., Department of Marine Biology, Texas A&M University at Galveston, Galveston, Texas 77550, U.S.A. [123, 126, 165]
REAL, Guy, Institut Universitaire de Biologie Marine, 2 rue du Professeur Jolyet, 33120 Arcachon, France [111]
REAL-TESTUD, Anne-Marie, Laboratoire de Biologie des Invertébrés Marins et Malacologie, 55 rue de Buffon, 75005 Paris, France [111]
REEDER, Richard L., Faculty of Biological Science, University of Tulsa, Tulsa, Oklahoma 74104, U.S.A. [165, 166]
REES, Bernard B., Department of Environmental, Population and Organismic Biology, University of Colorado, Campus Box B-334, Boulder, Colorado 80309-0334, U.S.A. [150]
REHDER, Harald A., [no address given] [143]
REID, Robert N., U.S. National Marine Fisheries Service, Northeast Fisheries Center, Sandy Hook Laboratory, Highlands, New Jersey 07732, U.S.A. [122]
REINA, Michele, Via Croce Rossa 159, 90144 Palermo, Italy [104]
REISCHÜTZ, Peter L., Lazarethgasse 5/15, A-3580 Horn, Austria [113, 153, 154]
REITSMA, N., Systematic Zoology Section, Leiden University, c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands [102]
RÉKASI, Jósef, Pannonhalma, Vár 2., H-9090, Hungary [158]
REMBECKA, Izabela, Silesian University, Faculty of Biology, 40-007 Katowice, ul. Bankowa 9, Poland [110]
REPETTO, Giovanni, Museo Civico «F. Eusebio» - 12051 Alba, Italy [104]
REX, Michael A., Department of Biology, University of Massachusetts, Boston, Massachusetts 02125, U.S.A. [149]
RICHARDSON, C.A., Animal Biology Group, Marine Science Laboratories, Menai Bridge, Anglesey, Gwynedd LL59 5EH, U.K. [119]

RICHNOVSZKY, Andor, Baja, Kölcsey u.l., H-6500, Hungary [158, 159]
RIEDEL, Adolf, Institute of Zoology, Polish Academy of Sciences, ul. Wilcza 64, 00-679 Warsaw, Poland [110, 118, 154]
RIISGÅRD, Hans Ulrik, Institute of Biology, Odense University, Campusvej 55, DK-5230 Odense M, Denmark [126]
RINALDI, Emidio, Via Marengo 29, 47100 Forlì, Italy [105]
RIOS, E.C., Investigador del Museo Oceanográfico de la FURG, Fundação Universidade de Rio Grande, RS, Uruguay [109]
ROBERTS, Kenneth J., Louisiana Cooperative Extension Service and Center for Wetland Resources, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A. [126]
ROBINSON, Anja, Department of Fisheries and Wildlife, Mark O. Hatfield Marine Science Center, Oregon State University, Newport, Oregon 97365, U.S.A. [123]
ROBINSON, John, 'B' Watch, S.C.S., 12. S.U., B.F.P.O. 53, United Kingdom [140]
ROBINSON, Keith, Division of Water Resources, New Jersey Department of Environmental Protection, Trenton, New Jersey 08625, U.S.A. [125]
ROBINSON, M. Elizabeth, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [124]
ROBINSON, S.M.C., Fisheries Research Branch, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada [122, 148]
RÖCKEL, Dieter, Neckaranlage 6, 6930 Eberbach/Neckar, F.R. Germany [113, 114]
RODHOUSE, Paul G., British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, U.K. [148]
RODRIGUEZ, Ma. Teresa, Departamento de Biología Animal, Facultad de Biología, Universidad de Santiago de Compostela, Spain [117]
RODRIGUEZ BABIO, C., Dpto. Zoología, Fac. C. Biológicas, Univ. Valencia; Dr. Moliner, 50 Burjasot 46100 Valencia, Spain [116]
RODRIGUEZ GIL, Luis, Instituto Tecnologico de Mérida, km. 5 Carretera a Progreso, 976 Mérida, Mexico [112]
ROLAN, E., Cánovas del Castillo 22 5°F, 36202 Vigo, Spain [103, 116, 117]
ROLDAN CORNEJO, Carmen, Cátedra de Zoología de Invertebrados no Artrópodos, Departamento de Zoología, Facultad de Biología, Universidad Complutense, Madrid 28040, Spain [117]
ROLLER, Richard A., Department of Biology, University of Wisconsin, Stevens Point, WI 54481, U.S.A. [96]
ROMER, Nidia S., Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A. [156]
ROMEY, William L., Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A. [126]
ROPER, Clyde F.E., Department of Invertebrate Zoology - Mollusks, Smithsonian Institution, National Museum of Natural History, Washington, District of Columbia 20560, U.S.A. [148]
ROPES, John W. [deceased] National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole Laboratory, Woods Hole, Massachusetts 02543, U.S.A. [126]
ROS, Joandomènec, Departament d'Ecologia, Facultat de Biologia, Universitat de Barcelona, Av. Diagonal, 645, 08028 Barcelona, Spain [116]
ROSTAL, David C., Portland State University, Department of Biology, Portland, Oregon 97207, U.S.A. [165]
ROTH, Barry, Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105, U.S.A. [166]
ROUSSY, H.P., Djibouti, East Africa [141]
ROWELL, T.W., Department of Fisheries and Oceans, Biological Sciences Branch, Scotia-Fundy Region, Halifax Fisheries Research Laboratory, P.O. Box 550, Halifax, Nova Scotia B3J 2S7, Canada [123]
RUBIO SALAZAR, Frederico, c/o Pintor Ribera, 4 - 46930 Cuart de Poblet, Valencia, Spain [116]
RUGGIERI, Giuliano, Dipartimento di Geologia e Geodesia della Università, Corso Tuköry 131, 90134 Palermo, Italy [104, 105, 106]
RUSSELL, Michael P., Department of Paleontology, University of California, Berkeley, California 94720, U.S.A. [172]
RYTHER, John H., Harbor Branch Foundation, P.O. Box 196A, Fort Pierce, Florida 33450, U.S.A. [122]
SAFRIEL, Uriel N., Department of Zoology, The Hebrew University of Jerusalem, Israel [101]
SAGE, Walter E., III, Department of Invertebrates, American Museum of Natural History, New York, NY 10024, U.S.A. [155]
SAITO, Hiroshi, Tokyo University of Fisheries, 4-5-7, Konan, Minato-ku, Tokyo 108, Japan [167]
SALAS, Carmen, Departamento de Zoología, Facultad de Ciencias, Universidad de Málaga, 29071 Málaga, Spain [116, 164]

SALGADO, Jennie, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile [164]
SAMATA, Tetsuro, Faculty of General Education, Azabu University, Sagamihara, Kanagawa, Japan [169]
SANDERS, James G., Academy of Natural Sciences, Benedict Estuarine Research Laboratory, Benedict, Maryland 20612, U.S.A. [124]
SAUL, LouElla R., Invertebrate Paleontology Section, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. [171, 172]
SAURIAU, Pierre Guy, Laboratoire de Biologie marine, Faculté des Sciences et Techniques 2, rue de la Houssinière, 44 072 Nantes Cedex 03, France [111]
SCAILLET, R., Av. Fr. Guillaume, 63, B-1140 Bruxelles, Belgium [98]
SCALERA LIACI, L., Istituto di Zoologia e Anatomia Comparata dell'Università di Bari, Italy [105]
SCARSELLI, Emilio, Instituto di Zoologia, dell'Università di Bologna, Italy [122]
SCHICK, Daniel F., Department of Marine Resources, West Boothbay Harbor, Maine 04575, U.S.A. [123]
SCHILDER, Franz A., [no address given] [132]
SCHMIDT, Nancy, Department of Geosciences, University of Arizona, Tucson, Arizona 85721, U.S.A. [171]
SCHNELL, Birgit & Waltraud, Leipziger Straße 20, 5014 Kerpen-Buir, F.R. Germany [115]
SCHÜTT, Hartwig, Haydnstraße 50, D-4000 Düsseldorf 13, F.R. Germany [100]
SCIOLINO, E., [no address given] [134]
SCOTT, Paul H., Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, Santa Barbara, California 93105, U.S.A. 171, 172]
SCOTT, P.J.B., Department of Geology, McMaster University, Hamilton, Ontario, L8S 4M1, Canada [119, 120]
SEAPY, Roger R., Department of Biological Science, California State University, Fullerton, California 92634, U.S.A. [171]
SEAWARD, D.R., Barn Court, Hamlet, Chetnole, Sherborne, Dorset, DT9 6NY, England, U.K. [118]
SEEMANN, R., Röbeler Chaussee 2, Waren (Müritz), 2060, D.R. Germany [152]
SELVIN, Rhonda, Bigelow Laboratory for Ocean Studies, West Boothbay Harbor, Maine 04575, U.S.A. [123]
SENDERS, J., 67, Rue de la Vallée, B-1050 Bruxelles, Belgium [98]
SEPHTON, Thomas W., Canada Department of Fisheries and Oceans, Science Branch, Gulf Region, Moncton, New Brunswick, E1A 9B6, Canada [123]
SHASKY, Donald R., 834 W. Highland Avenue, Redlands, California 92373, U.S.A. [172]
SHEARS, John, Dalhousie University, Department of Biology, Halifax, Nova Scotia, B3H 4J1, Canada [148]
SHEINBERG, Baruch, [no address given] [132, 134]
SHEN, Jiefen, Hwanghai Fisheries Institute, National Bureau of Aquatic Products, China [162]
SHUMWAY, Sandra E., State of Maine Department of Marine Resources, West Boothbay Harbor, Maine 04575, U.S.A. [123, 124]
SICARDI, Omar E., Sociedad Malacológica del Uruguay, Casilla de Correo No 1401, Montevideo, Uruguay [109]
SIDDALL, Scott E., Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794-5000, U.S.A. [125]
SIMPSON, Leonard, Portland State University, Department of Biology, Portland, Oregon 97207, U.S.A. [165]
SINGER, Benjamin (Solly), Sderot Ben Zion 44/3, 76410 Rehovot, Israel [142-146]
SIRENKO, B.I., Laboratory of Marine Investigation, Zoological Institute, USSR Academy of Sciences, University Embankment, 199164 Leningrad, 1, U.S.S.R. [150]
SIROIS, André, Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4J1 Canada [148]
SISSON, Richard T., Rhode Island Division of Fish and Wildlife, 150 Fowler Street, Wickford, Rhode Island 02852, U.S.A. [126]
SLOAN, N.A., Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, British Columbia, V9R 5K6, Canada [122, 126]
SMALLRIDGE, M.A., School of Biological Sciences, Flinders University, Bedford Park, South Australia, 5042 Australia [121]
SMITH, Douglas G., Museum of Zoology, University of Massachusetts, Amherst, Massachusetts 01003-0027, U.S.A. [156]
SMITH, Judith Terry, 1527 Byron Street, Palo Alto, California 94301, U.S.A. [171]
SMOUSE, D.T., Department of Biology, Oberlin College, Oberlin, Ohio 44074, U.S.A. [164]
SMRIGLIO, Carlo, Via di Valle Aurelia 134, 00167, Rome, Italy [104, 105, 106]

SONIAT, Thomas M., Department of Biological Sciences, University of New Orleans, New Orleans, Louisiana 70148, U.S.A. [126]
SORDI, M., Acquario Comunale "D. Cestoni", Livorno, Italy [102]
SPADINI, Valeriano, Via A. Toti 6, 52046 Lucignano (AR), Italy [104]
SPANIER, Ehud, Center for Maritime Studies, University of Haifa, Mount Carmel, Haifa 31999, Israel [136, 139, 147]
SPENCE, Margot J., Department of Zoology, University of British Columbia, Vancouver, V6T 2A9, Canada [164]
SQUIRES, Richard L., Department of Geological Sciences, California State University, Northridge, California 91350, U.S.A. [172]
STAHLNECKER, James, State of Maine Department of Marine Resources, West Boothbay Harbor, Maine 04575, U.S.A. [124]
STAIKOU, A., Section of Zoology, Department of Biology, University of Thessaloniki, 540 06 Thessaloniki, Greece [120]
STARMÜHLNER, Ferdinand, Zoologisches Institut der Universität Wien, Abteilung für Malakologie, Althanstraße 14, A-1090 Wien, Austria [113]
STAUB, Katherine C., Biology Department C-096, University of California - San Diego, La Jolla, California 92093, U.S.A. [149]
STEBBINS, Timothy D., Department of Biological Sciences, University of Southern California, Los Angeles, California 90089, U.S.A. [164]
STEPHEN, S.J., Marine Research Associates, St. Andrews, New Brunswick, Canada [148]
STÉVANOVITCH, Colette, 60 Esplanade Fléchambault, 51100 Reims, France [118]
STICKLE, William B., Department of Zoology and Physiology, Louisiana State University, Baton Rouge, LA 70803, U.S.A. [96]
STIPPROWEIT, Adelheid, Westfälische Wilhelmsuniversität, Fachbereich 24, Lehrgebiet Biologie, Fliednerstraße 21, D-4400 Münster, F.R. Germany [114]
STÖCKMANN-BOSBACH, Renate, Department of Zoology, University of Münster, D-4400 Münster, Hüfferstrasse 1, F.R. Germany [120]
STONEHAM, Hedy, Suva, Fiji [133]
STRACK, H.L., Hoeksestraat 8a, 3036LL Rotterdam, Holland [117]
STRAIN, Charles H., Department of Biology, University of the South, Sewanee, TN 37375, U.S.A. [148]
STRANKS, T.N., Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia [148]
STRZELEC, Malgorzata, Silesian University, Faculty of Biology, 40-007 Katowice, ul. Bankowa 9, Poland [110]
STUMMER, Anton, Kremserstraße 56, A-3511 Hörfarth, Austria [113]
SUGAWARA, Yoshio, Department of Fishery Science, Faculty of Agriculture, Tohoku University, Tsutsumidori-Amamiyamachi, Sendai, 980, Japan [168]
SUN, Bolun, Jienzhou Fisheries Institute, China [163]
SWEENEY, Michael J., Department of Invertebrate Zoology - Mollusks, Smithsonian Institution, National Museum of Natural History, Washington, District of Columbia 20560, U.S.A. [148]
SYSOEV, A.V., A.N. Severtzov Institute of Animal Evolutionary Morphology and Ecology of the USSR Academy of Sciences, Lenin Avenue 33, Moscow 117071, U.S.S.R. [99]
SZÖRÉNYI, László, Sopron, Határór u.13.I/5, H-9400, Hungary [159]
TABANELLI, Cesare, Via Testi, 4. 48010 Cotignola (RA), Italy [105]
TAN, Tien-hsi, Institute of Zoology, National Taiwan University, Taipei, Taiwan 10764, Republic of China [108]
TAN TIU, Antonieto, Harbor Branch Oceanographic Institution, Ft. Pierce, Florida 33450, U.S.A. [166]
TANG, Dehua, Sanitary and Anti-epidemic Station of Wufeng County, China [162]
TANG, Guozhu, Institute of Parasitic Diseases, Hupei Academy of Medical Sciences, China [162]
TARDY, Jean, Laboratoire de Biologie et Biochimie Marines, Univerité de Poitiers, I.U.T. rue de Roux, 17026 La Rochelle Cedex, France [111]
TATEWAKI, Reiko, Department of Biology, Shimane Medical University, Japan [168]
TAYLOR, Dwight W., Department of Geology, Oregon State University, Corvalis, Oregon 97331, U.S.A. [150]
TAYLOR, John D., British Museum of Natural History, Cromwell Road, London SW7 5BD, U.K. [151]
TAYLOR, Lawrence J., Department of Anthropology and Sociology, Lafayette College, Easton, Pennsylvania, U.S.A. [125]
TEMPLADO, José, Museo Nacional de Ciencias Naturales, José Gutiérrez Abascal 2, 28006, Madrid, Spain [120, 151]
TETTELBACH, Lisa Petti, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460, U.S.A. [126]

THOME, Jean-Pierre, Laboratoires de Morphologie, Systématique et Ecologie animales (Prof. Ch. Jeuniaux), Institut de Zoologie, Université de Liège, 22, Quai van Neneden, B-4020 Liege, Belgium [112]
THOMPSON, Fred G., Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A. [150]
THOMPSON, K., Seakem Oceanography Ltd., 2045 Mills Road, Sidney, British Columbia, V8L 3S1, Canada [123]
THOMPSON, T.E., Zoology Department, University of Bristol, Bristol, England, U.K. [119, 120, 121]
TIBA, Ranji, Otomomachi, Rikuzen-takata City, Iwate Pref., Japan [107, 157]
TIU, Antonieto Tan, Harbor Branch Oceanographic Institution, Inc., Division of Applied Biology, 5600 Old Dixie Highway, Fort Pierce, FL 34946, U.S.A. [96]
TOLL, Ronald B., Department of Biology, University of the South, Sewanee, TN 37375, U.S.A. [96, 148]
TOMIYAMA, Kiyonori, Ecological Zoology, Department of Biology, Tokyo Metropolitan University, Fukazawa, Setagaya-ku, Tokyo 158, Japan [169]
TONG, Baofu, Institute of Oceanology, Academia Sinica, China [163]
TOURARI, A.L., Laboratoire d'Ecologie, 1 Rue des Récollets, 57000 Metz, France [111]
TRIGO TRIGO, Juan E., Fray Rosendo Salvado, 13, 3°, Santiago de Compostela, Spain [116]
TROTTER, D., Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6, Canada [148]
TROWBRIDGE, Cynthia D., Department of Zoology, Hatfield Marine Science Center, Oregon State University, Newport, Oregon 97365, U.S.A. [171, 172]
TRUCHET, Michel, Laboratoire d'Histophysiologia Fondamentale et Appliquée, Unité Associée au C.N.R.S. No. 680, Université Pierre et Marie Curie, 12 rue Cuvier, 75005 Paris, France [149]
TSURIEL, P. Shraga, Weizmann Street 35, Nahariya, 22 404, Israel [130-137, 139, 141, 142, 143, 145]
TURSCH, B., Collectif de Bio-écologie, Faculté des Sciences, Université libre de Bruxelles, 50, Av. F.D. Roosevelt, 1050 Brussels, Belgium [97, 98, 99, 166]
TUTSCHULTE, Theodore C., Department of Biological Sciences, University of California, Santa Barbara, California 93106, U.S.A. [166]
TYLER, P.A., Department of Earth Sciences, University College, Singleton Park, Swansea, SA2 8PP, U.K. [120]
UKELES, Ravenna, National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460, U.S.A. [126]
UOZUMI, Kenji, 4451-10, Fukuma-machi, Munakata-gun, Fukuoka Pref., 811-32, Japan [169]
UPATHAM, E. Suchart, Center for Applied Malacology and Entomology, Department of Biology, Faculty of Science, Mahidol University, Rama VI Rd., Bangkok 10400, Thailand [149]
VAN BRUGGEN, A.C., Systematic Zoology Section, Leiden University, c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, NL 2300 RA Leiden, The Netherlands [103]
VAN GINKEL, Rob, Department of European and Mediterranean Studies, University of Amsterdam, The Netherlands [125]
VAN GOETHEM, J.L., Institut Royal des Sciences naturelles de Belgique, Section des Invertébrés récents, Rue Vautier, 29, B-1040 Bruxelles, Belgium [98]
VAN OSSELAER, C., Collectif de Bio-écologie, Faculté des Sciences, Université libre de Bruxelles, 50, Av. F.D. Roosevelt, 1050 Brussels, Belgium [98]
VAN URK, R.M., Rijksmuseum van Natuurlijke Historie, Postbus 9517, 2300 RA Leiden, Holland [158]
VARDINOYANNIS, K., University of Athens, Department of Biology, Section of Ecology and Taxonomy, Panepistimioupolis, Ilissia, GR - 157 71 Athens, Greece [154]
VARGA, András, Mátra Muzeum, Gyöngyös, Kossuth u.40, H-3200, Hungary [160]
VECCHIONE, Michael, National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, District of Columbia, 20560, U.S.A. [148]
VERDCOURT, Bernard, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, England, U.K. [100]
VERDUIN, A., c/o Rijksmuseum van Natuurlijke Historie, P.O. Box 9517, 2300 RA Leiden, Netherlands [102]
VERMEIJ, Geerat J., Department of Zoology, University of Maryland, College Park, MD 20742, U.S.A. [155]
VIAL, P., Quartier des Fontinelles, F-13810 Eygalieres, France [99]
VILAS, F., Universidad de Santiago, Colegio Universitario, Apdo. 874, Vigo, Spain [116]
VILLALBA, Antonio, Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [124]
VISEL, Timothy C., University of Connecticut at Avery Point, Sea Grant Marine Advisory Program, Groton, Connecticut 06340, U.S.A. [125]
VITALIS, Timothy Z., Department of Zoology, University of British Columbia, Vancouver, V6T 2A9, Canada [164]

VITTURI, R., Institute of Zoology, University of Palermo, Via Archirafi 18 -- 90123 Palermo, Italy [149]
VIYANANT, Vithoon, Center for Applied Malacology and Entomology, Department of Biology, Faculty of Science, Mahidol University, Rama VI Rd., Bangkok 10400, Thailand [149]
VOIGHT, Janet R., Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A. [148, 171]
VOLTZOW, Janice, Department of Biology, University of Puerto Rico, Rio Peidras, Puerto Rico 00931, U.S.A. [151]
VON DEN DRIESCH, Angela, Institut für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München, Schellingstraße 10/II, 8000 München 40, F.R. Germany [115]
VOSS, Gilbert L., Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida 33149, U.S.A. [148]
VOSS, Nancy A., Division of Biology and Living Resources, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A. [148]
WAGNER, H.P., Institut voor Taxonomische Zoölogie (Zoölogisch Museum), P.O. Box 4766, NL-1009 AT Amsterdam, The Netherlands [102]
WAITE, Thomas A., Department of Zoology, Ohio State University, Columbus, Ohio 43210, U.S.A. [120]
WALKER, Randall L., Marine Extension Service, University of Georgia, P.O. Box 13687, Savannah, Georgia 31416-0687, U.S.A. [124, 126]
WALKER, Sally E., Department of Paleontology, University of California, Berkeley, California 94720, U.S.A. [172]
WALLER, D.L., U.S. Fish and Wildlife Service, National Fisheries Research Center, P.O. Box 818, La Crosse, Wisconsin 54602-0818, U.S.A. [150]
WALSH, Dennis T., Aquacultural Research Corporation, P.O. Box AC, Dennis, Massachusetts 02638, U.S.A. [123]
WALSH, M., University of British Columbia, Vancouver, British Columbia, Canada [148]
WANG, Huiji, Nanjing Geology and Paleontology Institute, Academia Sinica, China [162]
WANG, Jianpeng, Freshwater Fisheries Institute of Shandong Province, China [161]
WANG, Lian-chen, Department of Parasitology, National Yang-Ming Medical College, Republic of China [108]
WANG, Xiyun, Institute of Microbiology, Jiangxi Academy of Science, China [162]
WANG, Yaoxian, Institute of Zoology, Academia Sinica, China [161, 163]
WANG, Zhixiang, Fisheries Committee of Weishan, Shandong Province, China [161]
WANG, Zichen, Dalian Fisheries College, China [163]
WARD, S., Department of Zoology, University of Melbourne, Parkville, Victoria, 3052, Australia [119]
WARÉN, Anders, Naturhistoriska Riksmuseet, Department of Invertebrate Zoology, Box 50007, S-10405 Stockholm, Sweden [105, 106, 151]
WATTS, M. Campbell, Department of Biology, University of Massachusetts, Boston, Massachusetts 02125, U.S.A. [149]
WEI, Liping, Yantai Fisheries School, Shandong Province, China [161]
WEI, Xinmin, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
WEI, Yiyao, South China Sea Institute of Oceanology, Academia Sinica, China [161]
WEITBRECHT, Barbara E., Department of Ichthyology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A. [165]
WEITLAUF, George, [no address given] [135]
WELLS, Fred E., Western Australian Museum, Perth 6000, Western Australia [119]
WERNER, Jürgen, Rübezahlweg 12, D-8206 Hinrichssegen, F.R. Germany [113]
WHELAN, Joseph G., III, University of Kentucky Medical Center, 800 Rose St., Lexington, Kentucky 40536, U.S.A. [149]
WHITCOMB, J.P., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [123]
WHITE, M.E., National Center for Atmospheric Research, Advanced Studies Program, Boulder, Colorado 80307, U.S.A. [123, 165]
WHITLATCH, Robert B., Department of Marine Sciences, University of Connecticut, Avery Point, Groton, Connecticut 06340, U.S.A. [124]
WIESE, Vollrath, Kleines Haus der Natur, Hinter dem Kloster 42, D-2433 Cismar, F.R. Germany [100, 114]
WIKFORS, Gary H., National Marine Fisheries Service, Northeast Fisheries Center, Milford Laboratory, Milford, Connecticut 06460, U.S.A. [126]
WIKTOR, A., Museum of Natural History, Wroclaw University, Sienkiewicza 21, 50-335 Wroclaw, Poland [152]

WILSON, E.A., Department of Oceanography, Texas A&M University, College Station, Texas 77843, U.S.A. [123, 165]
WITHSTANDLEY, Christopher A., Aquacultural Research Corporation, P.O. Box AC, Dennis, Massachusetts 02638, U.S.A. [123]
WOODRUFF, David S., Biology Department C-096, University of California - San Diego, La Jolla, California 92093, U.S.A. [149]
WU, Gang, Department of Biology, Southwest China Teachers College, China [161]
WU, Pingru, Fujian Institute of Oceanology, China [162]
WU, Shi-Kuei, University of Colorado Museum, Boulder, Colorado 80309, U.S.A. [172]
WU, Tiangming, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
WU, Wen-lung, Institute of Zoology, Academia Sinica, National Taiwan University, Taipei, Taiwan 11529, Republic of China [108]
XIA, Quanbin, Human Institute of Parasitic Disease Control, China [162]
XIA, Siguang, Department of Biology, Southwest China Teachers College, China [161]
XIANG, Xuansen, Sanitary and Anti-epidemic Station of Wufeng County, China [161, 162]
XIE, Shuibing, Human Institute of Parasitic Disease Control, China [162]
XU, Fengshan, Institute of Oceanology, Academia Sinica, China [161]
XU, Jitian, Fisheries Committee of Weishan, Shandong Province, China [161]
XU, Xingjian, Institute of Parasitic Diseases, Hupei Academy of Medical Sciences, China [162]
XU, Zhangchen, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
XUE, Jiang, Paragonimasis Research Laboratory, Yichang Medical College, China [161]
YAGÜE, Ma. José, Sociedad Cultural INSUB, Museo de Oquendo, Apartado 3031, 20080 San Sebastián, Spain [116]
YAMAMOTO, Aizou, 533, Izumi-macchi, Nagasaki City, 852, Japan [169]
YANG, Mingyue, Third Institute of Oceanography, National Bureau of Oceanography, China [163]
YANG, Shaojin, Sanitary and Anti-epidemic Station of Yichang County, China [161, 162]
YANO, Shigehumi, Sakaide Senior High School, Sakaide-shi, Kagawa-ken, 762, Japan [169]
YARON, Isaac, Research and Development Authority, Ben-Gurion University of the Negev, Beer-Sheva, Israel [131-138, 140, 141]
YIE, Wangji, Guangxi Marine Fisheries Institute, China [162]
YIPP, May W., Department of Zoology, University of British Columbia, Vancouver, V6T 2A9, Canada [165]
YOSHIOKA, Eiji, Seto Marine Biological Laboratory, Kyoto University, Shirahama, Wakayama 649-22, Japan [167, 169]
YOU, Yubo, Fujian Teachers University, China [163]
YOUNG, Richard Edward, Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822, U.S.A. [148]
YVORE, P., INRA, Station de Pathologie Aviaire et de Parasitologia, Unité de Protozoologie, 37380 Monnaie, France [120]
ZAOUALI, Jeanne, Institut National Agronomique, 43 av. Ch. Nicolle, Tunis, 1002, Tunisia [111]
ZAPATA, Bernardo, Escuela Superior Politecnica de Litoral, Facultad de Ingeniera Maritima y Ciencias del Mar, Guayaquil, Ecuador [126]
ZAVA, B., Institute of Zoology, University of Palermo, Via Archirafi 18 -- 90123 Palermo, Italy [149]
ZEIGLER, J.M., Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, U.S.A. [123]
ZEISSLER, Hildegard, Michael-Kazmierczak-Straße 3, Leipzig, 7022, D.R. Germany [114, 115, 152, 154, 160]
ZENG, Heqi, Department of Biology, Southwest China Teachers College, China [161]
ZENZIPER, Z., Department of Zoology, Tel-Aviv University, Israel [144]
ZHANG, Fusui, Institute of Oceanology, Academia Sinica, China [161, 162]
ZHANG, Li, Nanjing Institute of Geography, Academia Sinica, China [161, 162, 163]
ZHANG, Senkang, Paragonimasis Research Laboratory, Yichang Medical College, China [161, 162]
ZHANG, Suwang, Human Institute of Parasitic Disease Control, China [162]
ZHANG, Wenzhen, Institute of Zoology, Academia Sinica, China [161, 163]
ZHANG, Yuanrong, Shanghai Fisheries College, China [162]
ZHAO, Geng, Department of Biology, Shanxi University, China [162]
ZHOU, Deyen, Zhejiang Fisheries Institute, China [162]
ZHOU, Yibing, Department of Biology, Southwest China Teachers College, China [161]
ZHOU, Zhaoman, Shanghai Fisheries College, China [162]
ZHU, Huiguo, Institute of Parasitic Diseases, Hupei Academy of Medical Sciences, China [162]
ZHU, Xianggen, Nanjing Institute of Geology and Palaeontology, Academia Sinica, China [162]
ZHUANG, Qiqiang, Fujian Institute of Oceanology, China [162]

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NEWS AND ANNOUNCEMENTS

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MEETINGS

APRIL 10-12: SYMPOSIUM ON SLUGS AND SNAILS IN WORLD AGRICULTURE. Organized jointly by the Malacological Society of London and the British Crop Protection Council, this meeting will be held at the University of Surrey in Guildford, England, from 10-12 April 1989. The symposium will review the current economic status of land slugs and snails in world agriculture and will be of interest to those working on the control of slugs, on their behavior and physiology or on the exploitation of mollusks as a resource. For further details, contact Mrs. R.A. Bishop, The British Crop Protection Council, 20 Bridport Road, Thornton Heath, Surrey CR4 7QG, England, U.K.

MAY: MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. -- The 1989 annual business meeting of the Society for Experimental and Descriptive Malacology will be held in May, 1989. For further information, contact Dr. J. B. Burch, Secretary-Treasurer of the Society, P. O. Box 3037, Ann Arbor, Michigan 48106, U.S.A.

JUNE 19-24: CONCHOLOGISTS OF AMERICA CONVENTION -- The 1989 convention of the Conchologists of America will be held in San Diego, California, from June 19-24. For more information, contact Don Pisor, 10373 El Honcho, San Diego, California 92124, U.S.A.

Late JUNE to mid AUGUST: COURSE IN NATURAL HISTORY OF INVERTEBRATES. -- A field-oriented course on "Natural History of Invertebrates" will be taught by J. B. Burch at The University of Michigan Biological Station on Douglas Lake, Michigan, during the summer session (late June to mid August) 1989. Timothy A. Pearce will be assisting in the course. A prominent section of the course will deal with non-marine mollusks. For further information, write to the Director, University of Michigan Biological Station, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

JUNE 25-30: AMERICAN MALACOLOGICAL UNION AND WESTERN SOCIETY OF MALACOLOGISTS JOINT MEETING, 1989. -- The 55th annual meeting of the American Malacological Union and the 22nd annual meeting of the Western Society of Malacologists will be a combined meeting held in Los Angeles, California, June 25-30, 1989. Three symposia are planned: a full day symposium devoted to "Pelagic Gastropods," convened by Dr. Roger R. Seapy, a one and half day symposium on the "Systematics and Evolution of Western North American Land Mollusks," convened by Drs. F. G. Hochberg and Barry Roth, and a half-day symposium on "Scaphopod Biology," convened by Dr. Ronald L. Shimek. For further information, contact either Dr. James H. McLean, AMU President, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A. [telephone (213) 744 3377], or Dr. Hans Bertsch, WSM President, c/o the same address.

JULY 1-2: MEETING OF HUNGARIAN MALACOLOGISTS -- The annual meeting of the Malacological Section of the Educational Scientific Society of Hungary will be held in Baja on the 1st and 2nd of July 1989. The meeting will be co-sponsored by the József Pedagogical Higher University. The first day of the meetings will be devoted to scientific

reports of the members, and the second day with an examination of the peat bog at Kecel. For further information, contact Dr. A. Richnovszky, P. O. Box 48, 6501 Baja, Hungary.

Board members of the Malacological Section are Dr. L. Füköh, Dr. E. Krolopp and Dr. A. Richnovszky; Dr. G. Majoros is the Secretary.

AUGUST: INTERNATIONAL SOCIETY FOR INVERTEBRATE REPRODUCTION MEETING -- The International Society for Invertebrate Reproduction will meet in Nagoya, Japan, in August 1989. For more information, contact Professor David H. Montgomery, Department of Biological Sciences, California Polytechnic University, San Luis Obispo, California 93407, U.S.A.

AUGUST 27 to SEPTEMBER 2: UNITAS MALACOLOGIA, 1989. -- The Tenth International Malacological Congress will be held from 27 August to 2 September 1989 in Tübingen, Federal Republic of Germany. Papers on any aspect of malacology are invited for oral or poster presentation. Inqueries should be sent to the current president of Unitas Malacologica: Dr. Claus Meier-Brook, Tropenmedizinisches Institut der Universität Tübingen, Tübingen, F.R. Germany.

OCTOBER 25: FUNCTIONAL MORPHOLOGY OF THE MOLLUSCAN SHELL -- On 25 October 1989 the Malacological Society of London will hold a joint discussion meeting with the Palaeontological Association in the Department of Paleontology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, England, U.K. The topic for discussion will be "The functional morphology of the mollusc shell." Further details are available from Dr. J. D. Taylor, Department of Zoology, British Museum (Natural History), or from Dr. June Chatfield, The Gilbert White Museum, The Wakes, Selborne, Alton, Hampshire, GU34 3JH, England, U.K.

OCTOBER 25-28: TENTH MEXICAN NATIONAL CONGRESS OF ZOOLOGY. -- The Tenth National Congress of Zoology in Mexico will be held 25 to 28 October 1989 in Mexico City. Objectives of the congress include providing an academic forum to analyze, discuss, and disseminate information about the fauna of Mexico, identifying the principal problems facing Zoology in Mexico and proposing strategies toward their solution. For further information about the Congress or the Sociedad Méxicana de Zoología, contact Comite Organizador del X Congresso Nacional de Zoología, Secretaria de Publicaciones, Apartado Postal 101-11, C.P. 04530, México D.F., Mexico.

NOVEMBER 6-9: FRIENDS OF THE GASTROPODS ANNUAL MEETING -- The next annual meeting of the Friends of the Gastropods will be held during the Geological Society of America meeting in Saint Louis, Missouri, U.S.A., 6 to 9 November 1989. See p. 203 for more information about the Friends of the Gastropods.

1990: SECOND INTERNATIONAL CONGRESS ON MEDICAL AND APPLIED MALACOLOGY. -- The Second International Congress on Medical and Applied Malacology will be held in Seoul, Korea, in 1990. The purpose of the Congress is to bring together workers dealing with mollusks as mediators of parasitic diseases of man and domestic and other animals, mollusks as agricultural pests, as food, etc. The subjects that will be dealt with by the Congress are medical, veterinary, agricultural and shell fisheries malacology, and will include topics on biology (ecology, taxonomy, distribution, genetics, etc.) of mollusk hosts, pests and commercial mollusks, on mollusk-parasite relationships, on parasite faunas of mollusks, on snail control, etc. Those interested in attending the Congress should contact Prof. Pyung-Rim Chung, Department of Parasitology, Institute of Tropical Medicine, Yonsei University, C.P.O. 8044, Seoul, Korea. [**Please note that this is a change in venue from that previously announced.** The originally announced host for the 2nd Congress had to resign for health reasons.]

JUNE 18-22, 1990: WESTERN SOCIETY OF MALACOLOGISTS 23rd ANNUAL MEETING -- The 23rd Annual meeting of the Western Society of Malacologists will be held on the campus of the University of Washington, Seattle, Washington, June 18-22, 1990. There will be a symposium on the mollusks of Alaska. Field trips on June 22 will take advantage of some of the lowest tides of the year. For further information, contact Roland Anderson, The Seattle Aquarium, Pier 59, Waterfront Park, Seattle, Washington 98101, U.S.A. (phone 206-386-4347).

JUNE 3, 1990: AMERICAN MALACOLOGICAL UNION 56th ANNUAL MEETING -- The 1990 American Malacological Union annual meeting will be held during the week of June 3 at the Marine Biological Laboratory in Woods Hole, Massachusetts. Accommodations at motels (three) in the area will cost about $62.00 per night, and limited additional lodging will be available at the Swope Center and in student dorms. Meal plans will be available. A tentative symposium is planned on molluscan behavior, with a subsection emphasizing neurobiology. For more information, contact the 1990 president of AMU, Dr. Roger T. Hanlon, Marine Biomedical Institute, University of Texas Medical Branch, 200 University Boulevard, Galveston, Texas 77550-2722, U.S.A.

JOURNALS AND PUBLICATIONS

APEX, THE JOURNAL OF THE SOCIÉTÉ BELGE DE MALACOLOGIE. The Société Belge de Malacologie has announced that its publication for thirteen years, the *Informations Scientifique de la Société Belge de Malacologie*, has adopted a new style, a more scientific content and a new name, *Apex*. The following statement appeared in the first issue of *Apex*: "We feel privileged to introduce our new publication, *Apex*, which marks a turning-point in the activity of our society. This is not the first change we have undergone in nearly 20 years of existence. Since December 1966, our association has published a monthly bulletin [*Arion*], which is a true link between the members and a source of information of different kinds ... . Five years later, in January 1972, our society was conferred the legal status of a non-profit organization and at the same time, *Informations* was born ... . This publication, which has been printed for 13 years now, had a more scientific ... aim, whereas *Arion* was devoted to more general news. During all this time, we have tried to improve both the quality and production of the subjects. Photographic plates first ... appeared to illustrate the text, and soon the electronic stencil system was given up in favour of offset reproduction, and for two years now glossy paper has been used.

"The board of our society aimed at yet a higher status and decided to produce *Apex*. ... The latter is replacing *Informations* on a quarterly basis. ... We also wish to enlarge our audience, in Belgium as well as abroad." Articles in the new journal are published in any one of five languages: French, Dutch, English, German or Spanish. For further information, contact Monsieur J. Buyle, Av. M. Maeterlinck 56, B-1030 Brussels, Belgium. The tables of contents of *Apex*, from its beginning to now, are reproduced on pp. 97-99 of this issue of *Malacological Review*.

JOURNALS OF THE ISRAEL MALACOLOGICAL SOCIETY. -- In the past, *Argamon* has been the journal of the Israel Malacological Society, and *Levantina* has been the Society's newsletter. The Society has now announced a change in the status of the two publications. Henceforth, *Argamon* will be reserved for monographs (larger discourses on single subjects) and *Levantina* has been elevated to the status of the Society's regular journal (replacing *Argamon* in this respect). For further information about the two journals, contact Mr. Henk K. Mienis, Kibbutz Netzer Sereni, 70-395, Israel. The contents of the last issue of *Argamon* will be found on p. 101 of this issue of *Malacological Review*; the complete contents to date of *Levantina* will be found on pp. 129-147.

PUBLICATIONS OF THE SOCIETÀ ITALIANA DI MALACOLOGIA. -- *Bollettino Malacologico* is the quarterly scientific journal published by the Società Italiana di Malacologia. This journal is devoted to all aspects of malacology, but with special emphasis on Mediterranean mollusks. The Società's bimonthly newsletter is "Notiziario SIM." *Bollettino Malacologico* and "Notiziario SIM" go to members of the society around the world. The annual fee for membership in the Società Italiana di Malacologia is US$ 55.00, plus an additional US$ 2.00 for initial registration. Airmail delivery of the journal is optional and at extra cost. For further information, write to Società Italiana di Malacologia, Viale Gadio 2, 20121 Milano, Italy. The contents of the last issues of *Bollettino Malacologico* are shown on pp. 104-106 of this issue of *Malacological Review.*

CATOLOGO DEI MOLLUSCHI MARINI DEL MEDITERRANEO. -- The next edition of the *Catologo dei molluschi marini del Mediterraneo* [Catalogue of the Mediterranean Marine Molluscs] has been announced by the Società Italiana de Malacologia. This volume of more than 400 pages is scheduled for publication in 1989. It will include, beside the systematic list of molluscs with an up-to-date nomenclature, a rich list of synonyms, so that the reader can easily find correct species names even though using an out-dated nomenclature. Anyone interested in purchasing this catalogue should contact the Società Italiana de Malacologia, c/o Acquario Civico, Viale Gadio 2, 20121 Milano, Italy.

NEW POLISH SERIAL PUBLICATION ON MOLLUSKS, *FOLIA MALACOLOGICA.* -- A new serial publication on mollusks, *Folia Malacologica*, was initiated in Poland in 1988. The first in the series is a monograph in English by Andrzej Falniowski on "Hydrobioidea of Poland (Prosobranchia: Gastropoda)." The following statement appeared in this first issue. "Polish malacology has a rich tradition exceeding 100 years of research carried out in a number of scientific centres: at universities and museums of natural history. Researches ranged broadly from subfossil-Quaternary to contemporary faunae, and its results have been published in popular and scientific journals of zoology, ecology, geology, paleontology and allied sciences.

"In the last decades a vital development of various malacological research on a still broader range of issues has been observed due to a greater number of scientists involved and numerous scientific expeditions made with the participation of Polish scientists. Also we owe the development and progress in malacology to intensified research on the sediments of Quaternary period as well as on the state and changes of natural environment.

"Such a brilliant progress led in 1985 to the establishing of the Malacology Section at the Quaternary Research Committee of the Polish Academy of Science. The Section is active in all fields of malacological research on the Quaternary and contemporarily living molluscs. Its members are 50 scientists of all scientific centres of Poland. An attempt to issue an advanced scientific journal collecting and publishing papers on a broad range of malacological problems has succeeded in the establishing of *Folia Malacologica* published within the series of the Scientific Revue of the Academy of Mining and Metallurgy of Cracow. The Academy is a scientific centre with illustrious traditions of complex research on geology, and natural resources including the youngest geological period, as well as on the changes and anthropogenous degradation of natural environment. *Folia Malacologica* is edited by the publishing staff of research workers of five universities. The journal is to stimulate a broad interchange of experience, data and information on malacology. Two volumes in the Congress languages are going to be published yearly."

The contents of *Folia Malacologica* are shown on p. 110 of this issue of *Malacological Review.*

JOURNAL FOR MEDICAL AND APPLIED MALACOLOGY. -- The first volume of a new journal, the *Journal for Medical and Applied Malacology*, which addresses medical and applied aspects of malacology, will be released in 1989. The first volume will contain the proceedings of the First International Congress on Medical and Applied Malacology, which was held in Monterrey, Mexico, in 1987. The second volume, also scheduled for release in 1989, will contain contributed papers which have been submitted since the First Congress. The third volume is scheduled for 1990. Subscription price for the journal is US$ 40 for institutions and US$ 25 for private individuals (postpaid for mailing addresses in the U.S.A). Subscribers outside the U.S.A. must add and additional US$ 3 for postage and handling.

SUPPLEMENT 4 OF *MALACOLOGICAL REVIEW*: *PROSOBRANCH PHYLOGENY*. -- In December 1988, *Malacological Review* published its fourth supplement, *Prosobranch Phylogeny*, edited by Dr. Winston F. Ponder of the Australian Museum, Sydney, Australia. This hardbound book of 346 pages contains the proceedings of a symposium of the Ninth International Malacological Congress held in Edinburgh, Scotland, in 1986. The book contains four major sections: "Evolution and relationships of major groups"; "Relationships within single families or small groups of families"; "Evolution of characters and processes"; and "Appendix and indexes." Authors include Klaus Bandel, Rüdiger Bieler, Luis P. Burnay, Karl Edlinger, Gerhard Haszprunar, John M. Healy, Carole S. Hickman, Richard S. Houbrick, David R. Lindberg, Angel A. Luque, James H. McLean, Noel J. Morris, P. E. Penchaszadeh, Winston F. Ponder, Elizabeth Rath, John D. Taylor, José Templado, Janice Voltzow and Anders Warén.

This book is the most up-to-date reference on systematic relationships, classification and evolution in the gastropod subclass Prosobranchia. *Prosobranch Phylogeny* may be ordered from *Malacological Review*, P.O. Box 3037, Ann Arbor, Michigan 48109, U.S.A., or from *Malacological Review*, P.O. Box 637, Niwot, Colorado 80544, U.S.A. Price: US$ 48 (postpaid).

WALKERANA. -- *Walkerana*, founded in 1980, is a malacological publication of the POETS Society, sponsored by the Mollusk Division, Museum of Zoology, The University of Michigan. The journal is named in honor of the Godfather and major benefactor of the Mollusk Division, Dr. Bryant Walker (1876-1929). *Walkerana* is closely affiliated with the international journal *Malacological Review*.

Walkerana is open to publication by any author regardless of country, and does not limit the topic or the size of papers it publishes. Also, it does not make payment of page charges a prerequisite for publication. However, all manuscripts are reviewed by competent authorities before decisions are made regarding acceptance for publication. Recent articles have come from Argentina, Cuba, France, Korea, Thailand and the U.S.A. Currently, each volume contains approximately 300 pages. Three volumes (including the numbers currently in press) have been published. *Walkerana* is published irregularly, depending on material available for printing. (Its volumes do not necessarily correspond to calendar years.)

Walkerana is sold by complete volumes only, *i.e.*, individual numbers of any volume are not sold separately. The prices of back volumes and the current volume are given below.

Prices (postpaid) for *Walkerana*:

		Private Individuals	Institutions
Walkerana, Vol. 1, Nos. 1, 2, 3*, 4, 5	1980-1983	US$ 40	US$ 60
Walkerana, Vol. 2, Nos. 6**, 7, 8	1984-1987	US$ 25	US$ 40
Walkerana, Vol. 3, Nos. 9, 10	1988-1989	US$ 25	US$ 40
Walkerana, Vol. 4, Nos. 11§, 12§§	1989-1990	US$ 25	US$ 40

Walkerana, Vol. 1, Nos. 3* and 4, and Vol. 2, No. 6**, jointly constitute "*North American Freshwater Snails.*" These three issues may be purchased† as a unit from Malacological Publications, P.O. Box 193, Hamburg, Michigan 48139. Cost: $30.00, plus $4.00 for postage and handling.

* Currently not in print; Vol. 1, No. 3, will be available after May 31, 1989.
** Currently not in print; Vol. 2, No. 6, will be available after May 31, 1989.
† *North American Freshwater Snails* will be available after May 31, 1989.
§ Will appear in the summer of 1989.
§§ Will appear in the fall of 1989.

A CLASSIFICATION OF THE LIVING MOLLUSCA, assembled by Kay Cunningham Vaught, edited by R. Tucker Abbott and Kenneth J. Boss, xii + 189 pp., 1989. American Malacologists, Inc., P. O. Box 2255, Melbourne, Florida. "With the proliferation of new taxa proposed over the last twenty years, there has long been a need for a current list of supraspecific names in the Mollusca. Several well illustrated synoptic outlines appeared some years ago, such as Thiele's *Handbuch der systematischen Weichtierkunde* and the *Handbuch der Paläozoologie* by Wenz and Zilch. More recently, Franc in the *Traité de Zoologie*, Boss in the *Synopsis and Classification of Living Organisms*, and Vokes in his *Genera of the Bivalvia* have partially accomplished this task. ... Now ... Kay Cunningham Vaught ... has provided us with an up-to-date framework of the systematics of the Mollusca." (R. Tucker Abbott and Kenneth J. Boss). Available from American Malacologists, P. O. Box 1192, Burlington, Massachusetts 01803, U.S.A. Plastic comb binding, US$ 17; hardback US$ 21; US$ 2 mailing charges.

PUBLICATIONS OF THE SOCIEDADE PORTUGUESA DE MALACOLOGIA. -- The Sociedade Portuguesa de Malacologia was created in June, 1980, and in 1982 the Sociedade published its first issue of the *Publicaçõnes Ocasionais da Sociedade Portuguesa de Malacologia*. Since then, 11 additional numbers have been published, the last (No. 12) appearing in November, 1988. The contents of the *Publicaçõnes Ocasionais da Sociedade Portuguesa de Malacologia* will be covered in the next issue of *Malacological Review* (Vol. 23, 1990).

SOCIETY NEWS

INTERNATIONAL SOCIETY FOR MEDICAL AND APPLIED MALACOLOGY. The International Society for Medical and Applied Malacology was organized in 1985 to address the needs of workers dealing with mollusks as mediators of parasitic diseases of man and domestic and other animals, with mollusks as agricultural pests, food, etc. Membership in the Society is open to any person or institution interested in medical and applied malacology. Annual membership dues (which include a subscription to the *Journal for Medical and Applied Malacology* and receipt of the Society's Newsletter) for private individuals is US$ 25 and for institutions is US$ 45. The Society's offices are in the U.S.A. (P.O. Box 2715, Ann Arbor, Michigan 48106), México (Apartado Postal 21-360, Coyoacán, C.P. 04000, D.F., México) and Korea (c/o Institute of Tropical Medicine, Yonsei University, C.P.O. Box 8044, Seoul).

ASSOCIATION FRANÇAISE POUR L'ETUDE DES MOLLUSQUES CONTINENTAUX – The French Association for the Study of Continental Mollusca has announced its formation and an ambitious program formulated at its general Meeting on 12 November 1988. The purpose of the Association is to coordinate the efforts of all people who are, in one way or another, interested in land and freshwater molluscs of France and the European continent. The Association will publish a journal, with the first volume planned for 1989. It also plans to publish a regional atlas of mollusk distribution in France, and a

newsletter. Field meetings are planned for 25 March - 9 April 1989 (the Albères Mountains, eastern Pyrénées), 29 April - 1 May 1989 (Arcy-sur-Cure), 6-8 May 1989 (the Dombes Ponds, near Lyon), the summer (a week in the Larzac, north of Montpellier), and a number of one-day excursions. Annual membership fees are 50 francs for ordinary members and 30 francs for student members. The Association's address is c/o Múseum de Sciences Naturelles, 12 rue St. Michel, 28000 Chartres, France. Membership fees can be sent to the Treasurer, Sylvain Clanzig, 1 av. F. Vals, 11370 Leucate, France.

MALACOLOGICAL SOCIETY OF KOREA -- During May 1988, the Malacological Society of Korea sponsored two special lectures, one by Prof. J. B. Burch of The University of Michigan, Ann Arbor, Michigan, U.S.A., and the other by Prof. Ferdinand Starmühlner of the Universität Wien, Vienna, Austria. Dr. Burch's lecture, on 14 May 1988, was on "The freshwater pulmonate snail family Lymnaeidae." Dr. Starmühlner's lecture, on 25 May 1988, was on "Biology and ecology of tropical freshwater mollusks." Dr. Burch was presented with a plaque expressing the appreciation of the Malacological Society of Korea for his encouragement and advice to the Society during its formative stages.

The Malacological Society of Korea held a workshop at Mt. Chiri during 31 July through 2 August 1988. Activities included discussion sessions, collecting trips to Pia-Gol Valley and to the Seomjin River, and a visit to the Wawoo Trading Company at Kurye where Giant African snails (*Achatina fulica*) are being raised commercially.

At the Third Annual [1988] Meeting of the Malacological Society of Korea, Dr. Dong-Chan Kim was elected President of the Society for a two-year term. He succeeded Dr. Duk-Man Kim, who had served as the second president of the Society. Dr. Chin-Thack Soh was the Society's first president.

The 1989 Annual Meeting of the Malacological Society of Korea was held at the end of February. The main topic for discussion was molluscan biochemical systematics.

The Malacological Society of Korea is planning to publish a Society newsletter. It is anticipated that the newsletter will be sent, in addition to members of the Society, to all university libraries and biology departments, to other appropriate academic organizations and government offices, and to Korean middle and high schools.

The Malacological Society of Korea has now published three volumes (Vol. 1, for 1985; Vol. 2, for 1986; Vol. 3, for 1987) of *The Korean Journal of Malacology*. Vols. 4 (1988) and 5 (1989) are in preparation. Subscription price per volume is US$ 12 (postpaid). Correspondence regarding subscriptions should be sent to the Malacological Society of Korea (c/o Dr. Pyung-Rim Chung), Department of Parasitology, College of Medicine, Yonsei University, CPO Box 8044, Seoul, Korea. Correspondence regarding manuscript submission should be sent to the same address.

MALACOLOGICAL SOCIETY OF LONDON. -- The Malacological Society of London is essentially an international society that is centered in London. The objectives of the Society are to advance education and research for the public benefit by the study of molluscs from both pure and applied aspects. Anyone interested in the study of molluscs is welcome to apply for membership. Over the century since it was founded, the Society has maintained a continuous record of publishing important scientific papers on molluscs in the *Proceedings*, which evolved with Volume 42 (1976) into *The Journal of Molluscan Studies*. The *Journal* is published in annual volumes consisting of three parts which are received by fully-paid members and student members as they are issued. The annual subscription for Ordinary Members of the Society is £17.50 (overseas £25.00) and for student members is £7.50 (overseas £10.00).

The Malacological Society also publishes each year two issues of the "Bulletin of the Malacological Society of London," a newsletter for Society members. The editor of the "Bulletin" is Dr. June Chatfield. The last two issues of the "Bulletin" have included articles

on the origin of the Malacological Society's emblem [*Pomacea canaliculata*], research at Coleraine, molluscs protected by the Council of Europe Convention (the "Berne Convention"), and a report on advances in research on littorinid gastropods.

For further information about the Malacological Society of London, contact the Secretary, Dr. J. A. Crame, British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET.

MALACOLOGICAL SOCIETY OF THE PHILIPPINES. -- The Malacological Society of the Philippines has renewed its activities under its new President, Prof. Imelda F. Pagulayan. Other new officers are Vice-President, Mr. Jose Espejo, Jr.; Secretary, Ms. Ayolani de Lara (Acting, Ms. Doreen A. Darvin); Treasurer, Ms. Blesilda Viorge; Public Relations Officer, Mr. Roberto C. Pagulayan (Acting, Ms. Ruth Martinez); Editor, Ms. Lilia B. Querubin; Advisor, Dr. Bonificio C. Dazo; Honorary Advisor, Dr. J. B. Burch. The Society has recently drafted a new Constitution and By-Laws, and is holding fund-raising events. The Society is also presenting a seminar-lecture series in conjunction with the University of the Philippines Institute of Biology Seminar and Information Committee. A recent speaker was Dr. B. C. Dazo on "The role of malacology in the control of snail-mediated diseases."

FRIENDS OF THE GASTROPODS. "Friends of the Gastropods" is an informal group that exists to encourage and facilitate communication (and amusement) among students of fossil and living snails and snail-like organisms. The next annual meeting will be held during the Geological Society of America meeting in Saint Louis, Missouri, U.S.A., 6 to 9 November 1989. The newsletter, *Amici Gastropodorum*, contains summaries of research interests, new publications, and any other news or trivia of interest to gastropod workers. For further information contact Warren D. Allmon, Department of Geology, University of Southern Florida, Tampa, Florida 33620, U.S.A.

NEW DIRECTOR FOR THE DANISH BILHARZIASIS LABORATORY -- The Board of Directors of the Danish Bilharziasis Laboratory has appointed Dr. Niels Ørnbjerg Christensen as the new Director of the Laboratory. He succeeds Dr. Flemming Frandsen, who is now a professor at the Royal Danish Veterinary and Agricultural University. Dr. Thomas K. Kristensen has been appointed Deputy Director of the Laboratory. The budget of the Laboratory has been expanded in order to strengthen training and field research programs, and to broaden areas of responsibility to include other water-related vector borne diseases. In early 1989, the existing laboratory wing will be replaced by a three-floor building providing greatly expanded technical and other facilities.

SCHOLARSHIPS AND AWARDS

DELAWARE MUSEUM OF NATURAL HISTORY AWARDS FOR STUDENTS OF SYSTEMATIC MALACOLOGY -- The Department of Malacology at the Delaware Museum of Natural History announces the availability of two awards for students of systematic malacology: (1) The DMNH Trustees Award, up to $500, primarily intended to assist predoctoral and immediate postdoctoral students; and (2) The Jean Austin du Pont Memorial Award, up to $500, intended for all levels excluding postdoctoral students. These awards provide support for students conducting systematic studies of molluscs (leading to publication) who require access to the collections, laboratory and library of the DMNH Department of Malacology. Funds may be used for travel, subsistence and research costs. Applicants should submit a succinct research proposal (not exceeding two pages), a budget outline with indication of matching funds, and a supporting letter from faculty advisor(s). Mail to: Department of Malacology, Delaware Museum of Natural

History, P.O. Box 3937, Wilmington, Delaware 19807, U.S.A. Deadline for applications is May 1, 1989. Awards will be announced on June 1, 1989.

JACKSONVILLE SHELL CLUB SCHOLARSHIP -- The Jacksonville Shell Club announces the offering of a $500 grant-in-aid to a scholar who has demonstrated an interest and competence in natural science. The applicant must be enrolled in a program of study at an accredited U.S. institution at the college or post-graduate level. Special consideration will be given to those who are pursuing a curriculum in systematics, evolution, ecology and malacology. Applications are available from Harry Lee, M.D., JSC Scholarship Committee, 709 Lomax Street, Jacksonville, FL 32204, U.S.A. Deadline is May 1, 1989. Two letters of recommendation and an academic transcript are also required. Announcement of the recipient will be made on June 1, 1989.

DIRECTIONS TO AUTHORS

Malacological Review will publish the results of original work, of either descriptive or experimental nature, devoted primarily or exclusively to the study of mollusks, and will publish reviews of major research areas or malacological subjects. The articles must not be published elsewhere. *Malacological Review* aims to provide a common medium for such different aspects of malacology as anatomy, biochemistry, cytology, ecology, genetics, medical malacology, paleontology, physiology, taxonomy and zoogeography. The journal is especially concerned with maintaining scholarly standards. All manuscripts will be reviewed by competent scientists. Papers are judged on their contribution of original data, ideas or interpretations, and on their conciseness, scientific accuracy and clarity. Numerous and long tables, large numbers of figures, and pages in excess of 10 per article may be charged to the author at the current cost per page. Information concerning page costs will be transmitted to the author during the manuscript review process.

Manuscripts may be in English, French or German (English is preferred) and should follow *Malacological Review* style. All articles must contain a concise but adequate **abstract**, which should be an informative digest of significant content and should be able to stand alone as a brief statement of the conclusions of the paper. Manuscripts must be typewritten on one side of the paper, double spaced, with top and left-hand margins at least 3 cm wide, and are to be submitted in duplicate. Papers are accepted on condition that copyright is vested in the journal. No part of any article published in *Malacological Review* may be reproduced without the written permission of the publishers. All statements made and opinions expressed in any article are the responsibility of the author.

The publishers will set the text in the style adopted for the journal, and it would be helpful if authors would follow this style as closely as possible in the manuscript. Contributors are advised to follow the recommendations of the *Style Manual for Biological Journals*, obtainable from the American Institute of Biological Sciences, 2000 P Street, N.W., Washington, D.C. 20036, U.S.A. In particular, simplified practices, such as the following, are favored: numbers one through nine and numbers at the beginnings of sentences are written out; numerals are used when the number is followed by units of weight and measure; percentages following a number are expressed as %; units of weight and measure (mm, ml, kg, etc.) are abbreviated when preceded by numerals, and the abbreviations have neither a period nor an s in the plural.

Prospective authors are encouraged to submit a **computer disk** version of their manuscripts in addition to normal paper copies. This will speed processing and will reduce production costs. Disks can be either Macintosh or MS-DOS compatible and preferably in Microsoft Word, MacWrite or Wordstar formats, or saved from the word processor as a text (ASCII) file.

Latin names of genera and species should be underlined, and all Latin specific names should be followed by the authority when the name is first mentioned in the text or table. Generic names should be written out when first used in a paragraph; thereafter, in the paragraph, they are abbreviated when used with a specific name.

Illustrations must be carefully executed and so planned that they may be printed as figures of an appropriate size. The maximum size of a printed figure is 13.1 x 19.7 cm. Large illustrations must be accompanied by a smaller photograph for the editors. Drawings and lettering must be in black India ink or carbon black printing on white, blue tracing, or blue-lined paper. Charts should be drawn large enough to stand a reduction of one-half to one-third. This should be taken into consideration especially in relation to lettering. Letters and numbers must not be less than 1 mm in height, preferably larger, after reduction. A number of drawings or photographs may often be conveniently grouped together to fit a page. Photographs should be printed on white glossy paper, showing a full range of tones and good contrast.

Literature Cited. See current number of *Malacological Review* for desired form of citing. In particular, it should be noted that *"et al."* may be used in the text but not in the list of references at the end; in addition to the volume number, the complete page numbers of articles and books must be cited; for books, the publisher and city must also be cited. Journal names in references in the Literature Cited should be written in full, *i.e.*, they should not be abbreviated.

Voucher specimens of all species used in all types of research papers published in *Malacological Review* must be lodged in a recognized repository, *i.e.*, sample specimens of each species studied must be sent to a museum and, preferably, the registered numbers and full data of these specimens published. This insures that future workers will have easy access to this material and that species determinations will be accurate or can be checked.

Proofs should be returned with the least possible delay, and only essential corrections should be made. Other changes may be charged to the author. Authors are requested to pay particular attention to the checking of numerical matter, tables and scientific names.

Reprints (separates; off-prints) may be obtained at cost price if ordered at the time off-set proof is returned. Later orders cannot be considered. Order forms will accompany proof sheets sent to authors.

Correspondence. All manuscripts should be sent to *Malacological Review*, c/o Mollusk Division, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.